

PALMAR AND PLANTAR  
DERMATOGLYPHICS IN PRIMATES

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CHARLES MIDLO AND HAROLD CUMMINS









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## INTRODUCTION

As long ago as 1823 Purkinje remarked, after describing the configurations of the human finger tips and palms: "Also in the hands of apes, even in their prehensile tails, similar lines occur, the distinction of which adds to the knowledge concerning the characteristics of the species. Zoölogists, unless they consider them unimportant, will make them known further."

Little comprehensive work has been done in comparative dermatoglyphics since the classic studies of Whipple ('04), Schlaginhaufen ('05) and Kidd ('07). There have appeared only a few comparative studies, and these are mostly limited in scope: Bychowska ('30), on the palms of primates; Cummins ('33), a description of the macaque; Midlo ('35), on the tree shrew, *Tupaia*; Wolff ('37), a description of the chimpanzee, and ('38), on other primates; Mutrux-Bornoz ('37); an attempt to demonstrate the occurrence in man of degenerative stigmata resembling the conditions in non-human primates; Cummins and Spragg ('38) on the chimpanzee in detailed comparison with man; Dankmeijer ('38) on marsupials; and Midlo ('30, '38), dealing with primates generally.

We are prompted to resurvey the primates in the light of analytic methods and points of view developed in recent years and with the benefit of materials which are more extensive than those available to previous workers. It was expected that new information might be obtained in relation to morphology and that the utility of dermatoglyphics in tracing genealogical affinities could be put to test. The account is based upon observations of the palmar and plantar dermatoglyphics in thirty-six genera, which represent all the existing families and subfamilies of both the prosimians (*Lemuroidea*) and simians (*Anthropoidea*).

In all primates and in some other mammalian orders, especially marsupials, the skin of the palmar and plantar surfaces (and of the ventral surface of the tail in several New World monkeys) is distinctive in having a ridged or finely pebbled surface, hairs and sebaceous glands being absent. The pebbling (occurrence of islands, epidermal rings and "warts" — Whipple) represents a less advanced structural differentiation than does the presence of continuous epidermal ridges. Among the chief objects of study in a comparative survey of dermatoglyphics are determinations of the extent and distribution of areas presenting formed ridges and analysis of the variable arrangements of these ridges. Flexion furrows and other secondary folds are not elements of the dermatoglyphics.

In the majority of prosimians and in certain genera of New World monkeys, there occur in both palm and sole more or less extensive areas which lack ridges. Less frequently and less extensively is that the case in the Old World monkeys, while in higher primates the entire palmar and plantar surfaces are invariably continuously ridged, though often the ridges within flexion furrows are ill-formed. It should be noted, as emphasized by Whipple, that areas lacking formed ridges (presenting only islands, rings or "warts") occur in territories between pads or on their basal slopes.

In areas presenting definitely formed ridges there are distinguished three fundamental types of configuration: *open fields*, *patterns* and "*vestiges*". An open field is a succession of ridges which are straight or only gently curved. A pattern differs in that ridges are locally sharply recurved to form definite figures or designs. Such patterns are here classed under four main types: tented arches, loops, whorls and S-patterns. These types have their parallels in the more familiar patterns of the human finger tips, simple arches being excluded because they are open fields by definition. A vestige is a departure from the typical arrangement of an open field, its disarrangement of ridge courses suggesting a relationship to a pattern, as if a pattern were nascent or degenerated.



There remains to be defined another element of the configurations, the triradius ( $\delta$ ). At the conjunction of three systems of ridges having unlike courses a triradius occurs, appearing as a triangular consolidation of ridges. From each angle a radiant is extended, either as an actually continuous ridge or as one which may be projected according to prescribed conventions of tracing.

The topography on the palm and sole of discrete open fields, patterns and vestiges, and to a large extent the situations of triradii, are correlated with a systematic ordering of elevations of the volar surfaces (volar pads, walking pads or Tastballen). Each pad represents the site of a configurational field.

The morphologic plan of palmar and plantar configurational fields, characterized below, must be viewed as an idealized scheme. It is to be kept in mind that the basic plan of localized configurations is a composite representing discrete configurational fields (patterns, vestiges or open fields) which occur repeatedly at corresponding sites in different individuals and among different genera. Never in a single member is the scheme fully realized in the sense that all its units, thirteen in the palm or fifteen in the sole, actually appear as discrete elements. Occasionally the individualities of separate configurational fields are completely suppressed (e.g., *Hylobates*, fig. 499). The usual condition, as will be evident in scanning figures 5 through 593, is that several of the individual configurational fields are expressed in the single palm or sole. The identities of these fields are disclosed by their positions.

What is regarded as an especially significant analysis of the observations is presented under the heading of pattern intensity, where the characteristics of patterns are treated by a quantitative method designed for more ready comparison than is possible with the data as tabulated in a following descriptive section.

In the present analysis the characteristics of the several fields in the individual hand or foot are recorded, the results being summated for each genus. The reported observations



are confined to the palm and sole, digits being excluded on account of difficulties ordinarily attending examination in the preserved specimens.

As an expedient of brevity, the terms hand and foot, palm and sole, palmar and plantar, are used without regard to the objections which might be raised by terminological purists. The meaning as applied to primates will not be misunderstood, and under the circumstances there should be no uncertainty if on occasion the anterior paw of a strictly walking mammal be termed hand or palm! "Volar" is applied in its less restricted sense, embracing palmar and plantar surfaces. The expression "non-human" has been adopted, at the suggestion of Dr. A. H. Schultz, as a means of avoiding the implications of the commonly used terms "subhuman" and "infracuman" and in preference to more lengthy substitutes such as "primates other than man" (see Fulton, in the Introduction to Ruch's *Bibliographia primatologica*, '41). The technical equivalents of all common names of groups and genera appearing in the text are indicated in the pages which divide certain descriptive sections (pp. 27, 40, 46, 62, 78, 83, 90).

## MATERIAL

Exclusive of the much more extensive human series, the original material numbers 470 hands and 432 feet (as included in final tabulations; 7 hands and 7 feet of *Pongo* and 1 hand and 1 foot of *Daubentonia* also are included in supplementary descriptions, having become available too late for incorporation in all the analyses). In addition, 75 hands and 109 feet are analyzed from illustrations in the literature (Alix, 1867-1868; Hepburn, 1895; Whipple; Schlaginhaufen; Kidd; Keith, '24; Bychowska; Mutrux-Bornoz; Schultz, '37 b; Cummins and Spragg). The distribution among genera is listed in table 1. A detailed table, which identifies the source of each hand and foot included in the study, whether original or from the literature, is deposited in The Wistar Institute of Anatomy and Biology. This table lists the species name where known

and the identifying number of each specimen, or figure number and reference if from the literature; it states whether the member is right or left, and includes identifications of the hands and feet here illustrated.

Elliot's "A review of the primates" ('13) is adopted as the guide to taxonomy. Though we are well aware of its imperfections (see, for example, Yerkes and Yerkes, '29; Zuckerman and Fulton, '34), conformity to the Elliot classification and terminology seemed desirable. Being as it is the standard generally followed by others, a large share of the original material had been identified by reference to this

Table 1

Numbers of Hands and Feet Observed, Including Examples Illustrated in the Literature as well as Original Material.

	Original Material		From Literature			Original Material		From Literature	
	Manus	Pes	Manus	Pes		Manus	Pes	Manus	Pes
<u>Lemuroidea</u>	21	21	18	19	<u>Lasiopygidae</u>	145	140	30	30
Daubentonina	2	2	1		<u>Lasiopyginae</u>	127	125	26	28
Tarsius	7	7	1	2	Papio	18	17	12	9
Loris				1	Theropithecus			1	
Nycticebus	4	4	4	3	Cynopithecus			2	3
Rhodicticus	2	2			Magus	2	2		
Galago	2	2	2	2	Pithecus ( <i>Macaca</i> )	83	82	8	10
Lemur	4	4	9	11	Cercocebus	2	2	2	3
Propithecus			1		Lasiopyga	16	16	1	3
					Erythrocebus	6	6		
<u>Anthropoidea</u>					<u>Colobinae</u>	18	15	4	8
<u>Callithrichidae</u>	20	19	6	4	Pygathrix	13	12	2	1
Seniocebus	2	2			Nasalis	2	2		
Leontocebus	2	2	1		Colobus	3	1	2	1
Oedipomidas	14	13	2	1	<u>Hylobatidae</u>	46	41	1	20
Callithrix	2	2	3	3	Hylobates	44	39		7
<u>Cebidae</u>	132	118	15	17	Symphalangus	2	2	1	13
Alouatta	18	21	1	1	<u>Pongidae</u>	106	93	5	19
Saimiri	18	18	3	3	Pongo	16	15	3	5
Aotus	13	13			Gorilla	9	13	2	14
Ateles	46	35	3	2	Pan	81	65		
Lagothrix	4	4	2	1	<u>Hominidae</u>				
Cebus	33	29	6	10	Homo	1176	1322		
					<u>Totals (exclusive of Homo)</u>	470	432	75	109

work. For records in the literature named otherwise than according to Elliot, synonymies were determined from the lists in the Elliot review.

For the most part the specimens were examined in a preserved state, the preservation being chiefly in formalin. The ideal method of recording dermatoglyphics is in the form of

prints, but preservation almost invariably renders the skin unfit for printing. It was necessary, therefore, to resort to drawing, as explained on page 23. Prints were made of a few preserved specimens as well as a small number of living or freshly dead animals. Such prints were interpreted according to customary dermatoglyphic procedures, the result in each instance being transferred as a drawing within a standard outline as in the examples illustrated. Observations were made on the character of the pads and on other relevant features such as flexion furrows and the occurrence of areas presenting a lack of ridge formation; these were recorded in the form of notes and sketches.

The writers are indebted to a number of individuals and institutions for opportunity to obtain the materials for this study, and to the National Research Council for a Fellowship (Midlo) which made it possible to assemble records of material in several collections. We are particularly grateful to Dr. Adolph H. Schultz of the Johns Hopkins University, who made available during the tenure of the Fellowship the facilities of his laboratory and entire primate collection. Doctor Schultz also was so kind as to read the manuscript of this study and to offer invaluable suggestions bearing on terminology of primates and on the habits of several forms. We wish to acknowledge, further, the courtesies of access to material extended by the American Museum of Natural History, The Wistar Institute of Anatomy and Biology, the United States National Museum, the College of Physicians and Surgeons of Columbia University, the Bronx Zoological Garden, and the Johns Hopkins School of Hygiene and Public Health. For personal gifts of specimens we thank Dr. Ernest Carroll Faust of Tulane University and Dr. Dudley J. Morton of Columbia University. Finally, an expression of special gratitude is extended to Miss Genevieve Lee, who prepared for reproduction finished copies of the many original drawings and composed the lettered tables.

## DESCRIPTIVE MORPHOLOGY

## EPIDERMAL RIDGES

## DISTRIBUTION AND FUNCTIONS

Whipple devotes a large share of her study to a consideration of the morphology and evolutionary history of epidermal ridges, comparing her own findings with those of previous workers, especially Blaschko (1884, 1887), Klaatsch (1888), de Meijere (1894) and Reh (1894). The detailed construction of single ridges and of their forerunners is of little immediate interest, but their history among mammals provides an important orientation for interpreting the distribution of fully formed ridges in primates. Whipple points to the occurrence, on the summits of pads, of ridges in forms as low as marsupials, an edentate (*Myrmecophaga*) and some rodents (the wood-rat *Neotoma*, and *Sciurus*). In prosimians (*Galago* and *Lemur*) completed ridges are more extensive, but, according to her, still limited to the surfaces of pads, while in most simians the entire palmar and plantar surfaces are marked continuously by formed ridges. The sequence of stages of ridge evolution gives evidence that ridges are modified scales, and Whipple ascribes their conversion to ridge structure to factors associated with the functioning of contact surfaces. She writes:

“In ancient mammals the larger part of the surface of the body was covered with imbricated scales. Each of these scales or scale elements possessed, associated with it, a hair (or hair-group) and a sweat gland, the position of each being constant with relation to the scale. In recent mammals the scales occasionally persist, especially on tails and paws, showing, however, more or less modification of the original type. . . . Upon the ventral chirodial surface, there developed in the early mammals or in the pre-mammalian forms, a definite arrangement of walking pads in three rows. . . . Over the pad surfaces which, because of their greater elevation, are brought in contact with external surfaces, a highly specialized friction skin is developed by the fusion into ridges of rows of modified scales, characterized by the loss of hair and by the hypertrophy

of their sweat glands. . . . With the lowering of the pads due to adaptation of the chiridium to prehension, the area of friction skin increased in proportion to the enlargement of the contact surface, until, in the majority of Primates, the entire chiridial surface has become covered by ridges, having separate scale units along the margin of the chiridium only."

Kidd, while not studying so exhaustively the ultimate detail of ridge structure, supplies descriptions of the extent of ridge formation which agree closely with those of Whipple. His view of the factors promoting the evolution of ridges is, however, a different one. He ('20) emphasizes that

"the disappearance of the rough, plain, nodular or corrugated epidermis [embracing structures antecedent to ridges] in mammals is coincident with increasing activity and intelligence in forms who employ or acquire a more delicate sense of touch in their hands and feet. The cruder response of structure to stimuli of friction and pressure, evident in the lower forms, is abandoned in the higher, as tactile delicacy in prehension comes more into play."

Dankmeijer's observations on the marsupials are important in the present connection. Different forms within the group exhibit great diversity in the presence and extent of ridge formation. He confines attention to the posterior member, with the aim of simplifying the desired correlations of structure and function. Dankmeijer accords special stress to the finding that epidermal ridges occur on the pads of all marsupials which use this member for grasping in greater or lesser degree, the entire planta being continuously ridged in *Phalanger maculatus*. In two genera of the *Phascolarctidae*, however, ridges are lacking even though the feet are primarily used in grasping; conversely, he points out, ridges occur in other mammals (e.g., some rodents, a few carnivores and insectivores) in which the posterior member is not used as a grasping organ.

In summary of the observations of the authors cited, it may be stated that the simians present the most consistent and most extensive ridge development. Kidd even suggests that this is a "character of ordinal rank", though he makes the



error of stating, as if no other form were comparable: "Of course its highest development is found in the hand and foot of man." The prosimians as a group exhibit a lesser expanse of ridging, here, as in the marsupials, largely confined to the pads. From the marsupials, genera could be selected to match closely the conditions in prosimians. Some insectivores, rodents, edentates and carnivores possess epidermal ridges, but their occurrence is sporadic in these orders rather than characteristic.

Our observations on the extent of ridged skin in primates agree in principle with those of previous workers, including ridge formation on the tails of *Alouatta*, *Ateles* and *Lagothrix*.

The prosimian genera are widely diverse with respect to the extent of ridge formation. In the six genera represented in our observations *Galago* shows the least extensive ridge formation; definitely formed ridges are confined to the apices and slopes of the pads, while elsewhere on the palm and sole the epidermis is studded with islands or with consolidations of these units forming the "warts" of Whipple. Progressive expansion of the ridged area is to be seen in *Perodicticus*, *Daubentonia* and *Tarsius*. In *Lemur* the extension has proceeded still further. The patches of ridged skin characterizing the central portions of the palm and sole are larger than in the genera just mentioned, and their component ridges are consistently aligned (admitting the tracing of general ridge directions through these regions, as illustrated in figs. 33-40). Except in flexion furrows and in an occasional palm showing deficient ridge formation in a portion of the central area, *Nycticebus* presents continuously ridged palmar and plantar surfaces.

All the genera of *Nycticebidae* which we have studied are included in Hill's rating of progressive specialization in this family (Lorisoids, Hill). He ranks *Loris* as the most primitive, and in order follow *Nycticebus*, *Perodicticus*, *Galago*. Our observations on the extent of ridged skin do not correlate with this order. *Nycticebus* is more advanced than *Loris* in having a complete covering of ridged skin in the foot, and

nearly complete in the hand. *Perodicticus* and *Galago*, however, are no further advanced than *Loris* with respect to this character. Granting Hill's generalization, which is based on other morphologic criteria, it appears that the extent of ridge formation may follow a more or less independent evolutionary course, perhaps because it is subject to a control by local functional factors.

The diversity of prosimians recalls the variability among marsupials described by Dankmeijer, though there is no genus presenting the extreme simplicity expressed in some marsupials by the complete absence of ridge formation. The range of prosimian variation finds also a parallel among the simians, though in that group complete ridge formation is the rule rather than the exception.

With reference to the extent of ridged skin, *Aotus* is the least advanced of all simians which we have examined. The apices and slopes of pads display fully formed ridges, but in other regions of the palm and sole only islands occur, commonly elongated and aligned in such a way as to suggest that but slight structural advance would bring about their conjunction end to end as ridges. In some other platyrrhines (*Saimiri*, *Oedipomidas*, *Leontocebus*, *Seniocebus*, *Cebus*) by far the greater area of the palm and sole is ridged but at least some individuals of these genera have regions lacking complete ridge formation. Such regions, in the palm, are in the distal part of its central portion (coinciding with the simian line). In the sole it is less commonly the central area which is thus distinguished, but the proximal heel region instead. The remaining platyrrhines and all catarrhines, except rarely in the *Colobinae*, have continuously ridged palmar and plantar surfaces, though even here epidermal ridges are often less distinctly and regularly constructed in the flexion furrows.

There are suggestive indications, in those platyrrhines exhibiting regionally incomplete ridge formation and in the *Colobinae*, that the foot is farther advanced than the hand toward the state of a completely ridged surface. Such greater advance is indicated by the fact that in the sole areas lacking

formed ridges are in general less extensive and less frequently present than in the palm of the same genus.

The common lack of complete ridge formation within flexion furrows, noted especially in the palm, and in even the higher primates including man, indicates the retention of more primitive epidermal characteristics in these zones. It is possible that incomplete ridge formation is associated with nonparticipation of such zones in the functions served by the more directly exposed contact surfaces, but it is possible also that the furrows are distinguished by local peculiarities of histogenesis with which function bears no relationship. The construction of epidermal ridges has been shown by Abel ('35, '36) to be disturbed occasionally in the finger tips of criminals, mental defectives and in some congenital defects such as spina bifida, oxycephaly and malformations of the hands. Irregularities of ridge formation exhibited in these cases closely resemble the irregularities occurring in flexion furrows. Abel's cases demonstrate arrests of epidermal-ridge differentiation, and it is conceivable that the differentiation of ridges in flexion furrows may be disfavored by influences which are developmentally peculiar to these regions.

Two chief functions have been ascribed to epidermal ridges. One concerns the increase of frictional service in locomotion and prehension, in recognition of which the areas so specialized have been designated "friction-skin" by Whipple and by Wilder. The other function is the heightening of tactile sensibility — indicated in the term "Tastlinien". Though considerable attention has been devoted to the question as to which of these functions may be preëminent, the decisions of those who have discussed the subject appear to have no secure support. It must be conceded that both functions are mediated by ridging of the skin, and for the lack of convincing evidences we are not inclined to subordinate one to the other. No attempt can be made to evaluate their relative importance without having a thorough knowledge of differential habits among the genera and differences of use of hand and foot in

the same genus. At present it is not even certain that epidermal ridges can be justly regarded as having a uniform functional service in all mammals which possess them.

#### RIDGE BREADTH

It is obvious, since ridges participate in the growth of the hand and foot, that determinations of generic characteristics of ridge breadth and comparisons of genera can not be made unless the material is standardized according to growth stages. Schlaginhaufen presents determinations of ridge breadth in several primates, but because he failed to indicate the growth status of all the animals, we introduce some comparative results obtained without exception from adults. Even in the case of man, information bearing on variation in ridge breadth is scanty. Cummins, Waits and McQuitty ('41) have investigated individual and regional variation in ridge breadth of the human hand. These authors obtain an indirect measure of ridge breadth by counting the number of ridges transected at right angles by a line of 1 cm. In the present determinations the same method is followed, though the observations are limited to a single region in the palm, the proximal portion of the hypothenar area ( $H^p$  as defined below). This area is found to be the most favorable for orienting the line of count at right angles to the ridges, and moreover it is an area which in the available material is consistently clearly imprinted. For the comparison, thirteen animals representing eleven genera are available in actual prints, as listed in table 2, and one human hand is added for completion of the series. With the limitation of numbers of individuals nothing can be done with the question of individual variation; our primary emphasis is on the absolute ridge count per centimeter and its relation to hand size. It has been shown by Cummins, Waits and McQuitty that in the human hand there is a slight negative correlation ( $-0.30 \pm 0.05$ ) between ridge count and hand length. It might thus be expected that there would be evidenced among the genera an inverse relationship between ridge counts per centimeter and hand lengths. A loose rela-

tionship of this order appears in the results (table 2), but as shown by the hand length/ridge-count index, and as already noted by Schlaginhaufen in the sole, there is no rigid proportionate relationship between the two measures. The scale of ridge counts arranged in the order of increasing hand lengths does not show a regular progression. Such irregularities, moreover, may be demonstrated among individuals in a single genus, not only in man (Cummins, Waits and McQuitty—counts in five palmar regions and finger tips, 200 individuals) but also in chimpanzee (Cummins and Spragg—counts of hypothenar region of twenty animals).

Table 2  
Counts of Ridges per Centimeter in the Palmar  
Hypothenar Area in Adults of Thirteen Genera—  
(arranged in the order of increasing hand lengths)

Genus	Hand length.cm.	Ridge count	Hand length $\times 100$
			Ridge count
Saimiri	5.2	31	17
Aotus	5.4	25	22
Cebus margarita	7.0	20	35
Cebus capucinus	7.1	22	32
Erythrocebus	8.2	24	34
Lemur	8.3	36	23
Pithecus ( <i>Macaca</i> )	9.1	25	36
Cercocebus	9.5	22	43
Lagothrix	10.5	30	35
Magus	10.9	21	52
Pygathrix	12.0	20	60
Pithecus ( <i>Macaca</i> )	12.3	16	77
Alouatta	20.0	27	74
Pan ( <i>Cummins &amp; Spragg</i> )	20.0	23.3	86
Homo ( <i>Cummins &amp; Spragg</i> )	20.0	17.8	112

The range of ridge counts in the series of thirteen genera is 16 to 36, and the range of hand lengths is 5.2 cm. to 20 cm. It may be noted, notwithstanding a trend toward an inverse relation between hand length and ridge count, that the varying hand lengths are not associated with proportionately different ridge counts. In the animal having the smallest hand length (Saimiri, 5.2 cm.) the count of ridges per centimeter is 31, while Lagothrix, with a hand length twice that of Saimiri,

has an equivalent ridge count, 30. Again, in two specimens with hand lengths nearly four times as great (*Alouatta* and *Pan*) the counts are but little smaller (27.0 and 23.3 respectively). Forms having practically equal hand lengths may exhibit quite different ridge counts, as in *Saimiri* and *Aotus*, *Erythrocebus* and *Lemur*, *Lagothrix* and *Magus*, *Alouatta* and man.

The range of ridge counts in the thirteen genera (table 2) approaches that of the Cummins and Spragg series of twenty chimpanzees (18.2 to 33.9), composed of animals of different ages in which the hand lengths range from 11.7 cm. to 22.0 cm. In a series of human hands with the same lengths, the ridge counts range from 15.9 to 26.5. The greater coarseness of ridges in the human hand as compared with chimpanzee thus indicates a generic difference in the breadth of ridges, occurring independently of hand length. The observations here reported on a series of genera, with disproportions of hand lengths and ridge counts, further indicate the existence of generically unlike tendencies in ridge breadth. The upper and lower limits of the observed ridge counts per centimeter, 36 and 16, probably at least closely approach the actual extremes of variation in ridge breadth. The breadths of epidermal ridges, like other dimensional characteristics, seemingly are fixed or limited by some fundamental genetic mechanism, and this mechanism is in part independent of hand size.

The hand length/ridge-count index was not used in the cited studies of human and chimpanzee palms. Because of this omission the index is now applied to the hypothenar area of these series, and the results are presented for comparison with the general primate material. From the latter material, table 2, two specimens are excluded (*Cebus capucinus* and the specimen of *Pithecus* first in the list) in order to confine this analysis to one representative of each genus. The 200 human subjects have indices ranging from class centers (5-unit classes) 72 to 152. The mean is 104.7 and the standard deviation 12.5; the coefficient of variation is 11.9. In chimpanzee the index ranges from 40 to 121. The mean is 55.9, the standard



deviation 6.7, and the coefficient of variation, 12.0. It will be evident, therefore, that notwithstanding the existence of finer ridges in the chimpanzee palm, the magnitudes of variation in the relation of hand length and ridge count are equivalent in man and chimpanzee. It will be recalled that the series of 200 human subjects is made up of young adults. The chimpanzee material comprises both adults and juveniles, indicating that the comparisons with man should be carried further to include a comparable group of human subjects. Such a group is available in the series of twenty individuals originally reported in the chimpanzee study. The indices here range from 51 to 126, the mean being 77.6. The standard deviation is 9.9 and the coefficient of variation 12.8. The variability is thus equal to that in the human series composed wholly of adults as well as to the chimpanzee material comprising both adults and juveniles.

In the collective primate series the index presents a much wider range, 17 to 112.<sup>1</sup> While the mean, 51.5, is not significantly smaller than that of the chimpanzee series, the variability is much more pronounced (standard deviation, 28.7; coefficient of variation, 55.7). These findings show that variability among genera, with respect to the proportion of hand length and ridge count per centimeter, is far greater than the variability within a genus or species.

It is possible that variations in breadths of epidermal ridges, both absolute and relative to hand length, would throw light on the problem of ridge function if the variations were carefully collated with differing habits of the animals. Apparently significant is the fact that the range of variation in absolute ridge breadth is quite limited, in spite of large differences among the genera in hand length and body size. This confined range of variability in the breadths of epidermal

<sup>1</sup> The upper limit of the hand length/ridge-count indices is raised slightly by the recent addition of four adult orangs, in which the average index is 117. The actual values are:  $21.7/21.5 = 101$ ;  $24.4/22.5 = 108$ ;  $24.3/21.5 = 113$ ;  $25.0/17.0 = 147$ . These results are not included in the statistical analysis of ridge breadth, but it may be noted that the finding in *Pongo* is in keeping with the generalizations stated in this section.

ridges, whatever may be the hand length and size of the animal, might suggest that the proper performance of their functions depends perhaps as much upon absolute size of the ridge structure as upon proportionate development of the ridges and bodily dimensions. A small animal may or may not have finer ridges than a larger one, but in any case its ridges are proportionately coarser, as if limits of ridge breadth were imposed by factors which are more or less independent of the regulation of body size. There must exist, in addition to this regulation of ridge breadth, some genetic mechanism which is concerned with the more specific determination of limits within a single genus. Chimpanzee, as before noted, possesses narrower ridges than man, and though our present observations are confined to one or at most two individuals of each genus, it is clear that still finer ridges occur in some other forms (table 2).

#### THE BASIC PLAN OF VOLAR PADS AND OF DERMATOGLYPHIC CONFIGURATIONS

The volar pads of primates have been studied by several workers, notably Kollman (1883-1885), Klaatsch, Hepburn, Whipple, Schlaginhaufen and Kidd ('07). These authors agree in a common plan of the typical mammalian pads, comprising three series of pad elevations: on the terminal segments of digits; a series of three or four interdigital pads lying in the distal region of the palm or sole; two more proximally situated pads, the thenar and hypothenar. In addition to this complement of typical pads, termed by Whipple primary, there occur in "some of the highly specialized forms such as *Galago* . . . extra pads, which, as they show no evidence of a general homology with pads of other orders of mammals, may be regarded as secondary developments arising from the peculiar needs of adaptation and will be referred to as secondary pads" (Whipple). As pointed out especially by Whipple and by Wilder (1897), alteration of the typical mammalian plan may occur through suppression of individual pads and expansion and fusion of neighboring pads. A fair

idea of variations in prominence of pads may be gained by inspection of figures 15-21 and 23-30 in the study by Schultz ('31). In spite of such departures the existence of a common systematic distribution of pads is clearly evident in a view of the primates as a whole, and it is occasionally closely approached in a single genus (as in *Aotus*, figs. 1 and 2).

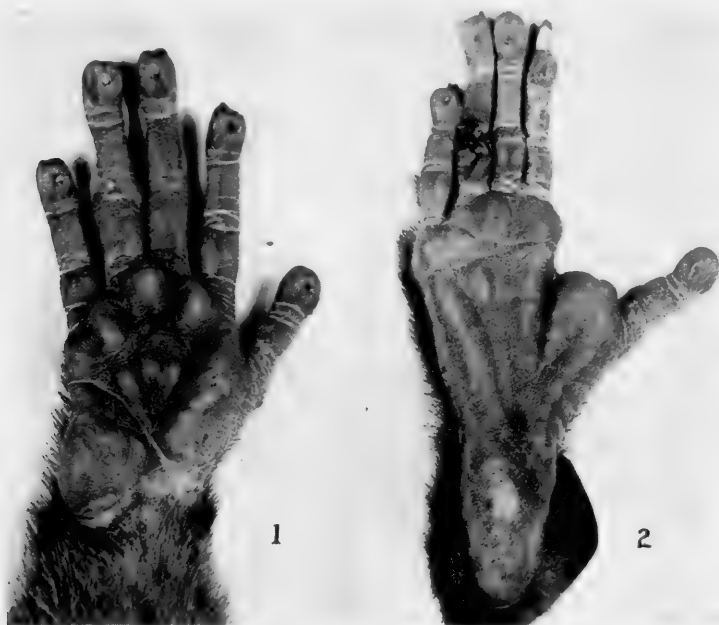


Fig. 1 *Aotus zonalis*, right manus, about  $\times 1$ . (From Schultz.)

Fig. 2 *Aotus zonalis*, right pes, about  $\times 1$ . (From Schultz.)

In our interpretation of the morphologic plan of the volar pads we have been guided not only by direct observation of the pads and their dermatoglyphic correlates in adult primates, but also by the history of pads in the human fetus (Cummins, '29), in the macaque (Schultz, '37 b), and in *Tarsius* (Hubrecht and Keibel, '07). The embryologic considerations are revealing since in the fetus the pad arrangement is observed in a primitive condition which may be obscured as development proceeds. The pad elevations of the fetus, moreover, are of

importance in reflecting the factors of differential growth which are responsible for the production of patterns. The combination of findings in the fetus and in the adult admits the construction of a comprehensive morphologic plan which comprises, in both palm and sole, seven marginally placed elevations of relatively constant occurrence. These pads, and their abbreviated designations, are:

H<sup>d</sup>, distal element of the hypothenar

H<sup>p</sup>, proximal element of the hypothenar

Th, thenar (in the sole having two elements, proximal and distal — Th<sup>p</sup> and Th<sup>d</sup>)

I	}	the interdigital series.
II		
III		
IV		

The locations of these pads correspond to configurational areas of the same names, as shown in figures 3 and 4.

As will be detailed in a following section, the morphologic plan is subject to considerable modification in individual genera. Among the modifications there should be noted especially the tendency of adjoining pads to fuse. H<sup>d</sup> and II<sup>p</sup>, for example, may be represented by a single eminence, H. Likewise, Th and I frequently are combined in one elevation.

Except in connection with elements of the hypothenar, no alterations of previous nomenclature of the primary border pads have been made. In his discussion of the fetal history of volar pads, Cummins ('29, fig. 1) distinguished two hypothenar pad elements, proximal and distal. What was then considered the proximal component alone is itself subdivided in the palm, as later recognized by the same author ('35 b). The elements which we designate herein as H<sup>d</sup> and H<sup>p</sup> are these subdivisions, while the fetal pad which Cummins had regarded as the distal hypothenar we now assign (as IV<sup>a</sup>) to the series of five subsidiary pads next to be mentioned. The palmar pad which we name H<sup>p</sup> is termed by Schlaginhaufen the carpal pad. In explanation of this altered terminology, it should be stated that the new designations appear to be more in keeping

with terms which may be fittingly assigned to primates generally.

Included in the basic plan here adopted are five smaller pads which had not been completely systematized heretofore: two ( $II^r$  on the radial side of II, and  $IV^u$  on the ulnar side of IV;  $II^t$  and  $IV^t$  corresponding in the sole) are located in association with the marginal set (*Nycticebus*, *Aotus*, fetal man); and three (respectively  $2^p$ ,  $3^p$  and  $4^p$ ) lie in the central area of the palm (*zentrale Ballen*, *Schlaginhaufen*) proximal to the three interdigital pads.

In summary, it may be stated that the pads fall naturally into two groupings, hereafter termed border pads and central pads. Distributed around the margin, the *border pads* include  $H^d$ ,  $H^p$ , Th, I,  $II^r$ ( $II^t$ ), II, III, IV, and  $IV^u$ ( $IV^t$ ). The *central pads* comprise  $2^p$ ,  $3^p$  and  $4^p$ . If the calcar elevation (C) be considered a true pad it would be assigned to the series of border pads, and perhaps specifically identified as an element of the hypothernar.

It is not intended to present a fully detailed description of the volar pads. The reader is referred to Klaatsch, Whipple, Kidd and Schlaginhaufen for more extended descriptions of their modifications in various genera. Our concern with pads is limited to their participation in a common plan of pads and configurational fields and to their influence on the production of specific ridge configurations. At this point attention may be called to the fact that forms which possess the most prominent volar pads (e.g., Old World monkeys) are characterized by the high degree of development and frequency of patterns. Conversely a form which presents little or no indication of well-marked pads (for example, *Hylobates*) shows a marked reduction in frequency and complexity of patterns. It does not follow that such inverse relationships of pads and patterns are inevitable, for in great apes and in man patterns of much complexity may occur in the absence of prominent pads. This lack of complete correspondence between pads and patterns in adult primates is explained below on a developmental basis. The ultimate correlation

between specific configurations of epidermal ridges, pads, and valleys of the volar reliefs has as its probable basis their developmental dependence upon common factors of differential growth (p. 157).

The basic plan of configurational fields (figs. 3 and 4) is in the main a counterpart of the pad disposition described above,

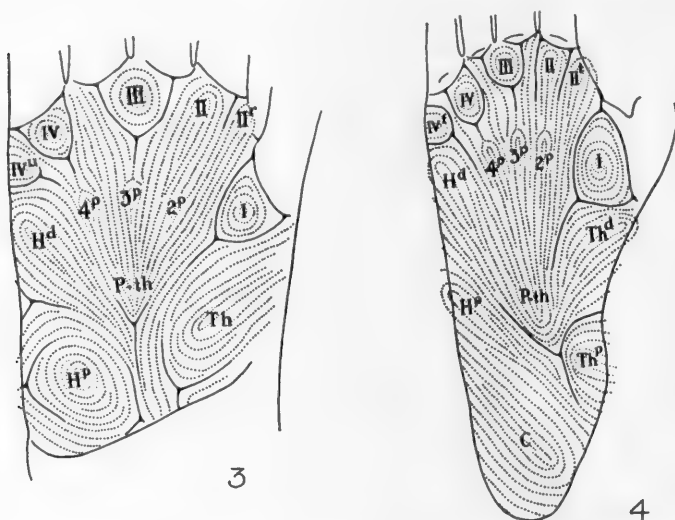


Fig. 3 Composite scheme of the palmar dermatoglyphics, illustrating the morphologic plan of configurational areas. I, II, III and IV are interdigital areas, designated by the respective numbers; II<sup>r</sup> is a field occasionally found on the radial side of II, and IV<sup>u</sup> represents a similar accessory feature in close relation to IV. The elements of the central area are termed 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>, emphasizing their proximal relation to the corresponding interdigital patterns. The hypothenar area is represented with separate distal and proximal components, H<sup>d</sup> and H<sup>p</sup>. The thenar (Th), occupying the thenar eminence, usually is separated from the hypothenar configuration by a definite parathenar configuration (P-th). Variable as are both configurations and volar pads, the conformity of configurational topography and the pads shown in figure 1 should be noted.

Fig. 4 Composite scheme of the plantar dermatoglyphics, illustrating the morphologic plan of configurational areas. With the exception of the necessarily different notations of accessory patterns II<sup>r</sup> and IV<sup>r</sup>, the distal, central and hypothenar portions of the sole correspond to the plan of the palmar dermatoglyphics. The thenar territory occasionally presents a separation of distal and proximal elements (Th<sup>d</sup> and Th<sup>p</sup>), and on the heel a calcar pattern (C) occurs occasionally.



and the nomenclature conforms as well. It must be appreciated, however, that for configurational fields as well as pads the representation is a composite or idealized scheme. No single palm or sole of any genus would present the complete series of patterns, though the full complement may be closely approached (e.g., *Aotus*, figs. 126-149).

In the sole there is one instance of failure of full conformity between the plan of pads and the plan of configurational fields. A defined calcar pad is lacking, but in the heel region a calcar pattern is of fairly frequent occurrence. The morphological identity of the calcar dermatoglyphic territory is obscure, but we agree with Wilder ('16) that it is perhaps best considered as a proximal extension of the hypothenar area. This homology holds true if based upon skeletal relationships alone, since in the palm the  $H^p$  territory extends into the level of the carpus, and the calcar dermatoglyphic area is similarly related to the tarsus. This proximally extended portion of the sole, however, does not bear a pad and hence is not to be considered strictly as the dermatoglyphic equivalent of the  $H^p$  pad area of the palm. While the whole calcar area may be interpreted as an extension of the hypothenar region, the pattern which it occasionally bears is a supplement to the morphologic plan, and it has no pattern homologue in the palm because homologies in configurational fields must be referred to pads; in the sole the  $H^p$  pad lies much farther distally. Calcar patterns are accordingly not included in the analyses of pattern intensity which follow, where comparisons between palm and sole are requisite. The only items of questioned homology of configurational fields in palm and sole involve the hypothenar, which is mentioned above, and the thenar. It is likely that the occasional separation of the plantar thenar configuration into proximal and distal elements is related to elongation of the sole, and that  $Th^d$  alone is homologous to  $Th$  in the palm. The proximal element,  $Th^p$ , might thus be compared to the similar association of  $H^p$  and the calcar region in the sole.

At the site of a pad a configuration of one or another morphological type may occur; in the construction of the drawings representing the basic plan it was of course necessary to select arbitrarily a specific configuration type for each of the areas. It should be mentioned also that the supplanting of patterns by open fields does not involve necessarily the loss of recognizable adherence to the basic plan. In the palm of *Tarsius* (figs. 9–12), for example, the open fields in the interdigital areas are separately indicated, each field lying on a discrete interdigital pad. Even in the lack of such discreteness of interdigital pads, as in the human palm (figs. 587–588), the morphological areas may still be recognized when the configuration is reduced to an open field, boundaries being provided by triradii and their radiants. When pad reduction is carried to an extreme (as in *Hylobates*, figs. 459–498) such boundaries of interdigital configurational areas are characteristically absent, but the occasional occurrence of boundaries, and even the rare appearance of a pattern, give sufficient basis for descriptive regional divisions corresponding to the fundamental plan.

Whipple designates as a “false pattern” one which lies in a depression rather than on a pad. These false patterns are in no sense less true patterns, as distinguished from open fields, than are patterns lying on pads. Whipple’s intent was to emphasize that such configurations are morphologically unrelated to the so-called primary and secondary patterns which occupy pads. The parathenar pattern conforms to her definition of a false pattern. It lies, whether in palm or sole, in the proximal portion of the central area, in the sunken region between the hypothenar and thenar eminences. Even when a pattern is not elaborated in this region the open field of the parathenar area is often distinctively outlined. The consistency of expression of a parathenar configuration, be it pattern or open field, may be interpreted as a correlate of the fairly uniform occurrence of a valley between the hypothenar and thenar eminences.

## OBSERVATIONS ON PADS AND PATTERNS

This section is devoted to illustrations and formulated descriptions of the dermatoglyphics. The illustrations are from our original material alone. The descriptions are based upon the specimens illustrated, other specimens from the original material and a considerable number of drawings in the literature. The individual hands and feet are identified, as to source and side, in a list which is deposited in The Wistar Institute of Anatomy and Biology.

The numbers of illustrations of hands and feet vary among the genera according to the amounts of material available. In genera represented by large series of observed individuals correspondingly large numbers of hands and feet have been selected for illustration, to secure comprehensiveness of these graphic records of variation. In most genera represented by limited numbers of specimens all the available hands and feet are illustrated. Left hands and feet are reversed in drawing, to obviate the difficulty of comparing the mirrored relationships of right and left members. All figures, therefore, appear as direct views of right members (or as contact prints of lefts).

The outlines of hands and feet do not conform to a fixed scale of sizes. They are the same outlines used by Midlo ('34) as standard illustrations of hand form and foot form. Dermatoglyphics are transfers within these standard outlines of original drawings or of interpreted prints made in the course of study. The first step in study of the actual hand or foot was to locate triradii and to trace the radiants extended from them. With these landmarks inserted in the outline, the courses of ridges were then traced in accord with direct observation. The tracing aimed to show only the general morphological characteristics of the configurations, distinguishing open fields, vestiges and the various pattern types without attention to the details of individual ridges. The same procedure was followed in the study of casts of two specimens of *Gorilla beringei*, one foot of each.

With few exceptions, the area in which the dermatoglyphics are drawn is confined to the palm and sole, portions of digits included in the outlines being left blank. Areas left blank on the palm or sole are regions lacking ridge formation (having only islands and epidermal rings), except in instances where a question mark is inserted to indicate that a scar or other defect renders impossible a reliable determination of the dermatoglyphics. In drawings of the soles of prosimians the proximal boundary of the area of ridged skin is limited by a line, the hairy heel region being either omitted or left blank.

In the formulated descriptions listed under each genus below, the frequencies of configuration types in each of the morphologically recognized areas are stated. Excepting man, where frequencies are in percentages, they represent the absolute numbers of the various configuration types.

The numbers of examples upon which the observations are based are variously placed in the descriptions. Where the entire series of hands or of feet available in the genus is utilized for all areas, the number is placed in the heading, in parentheses. It is often that one or more areas in a palm or sole must be omitted in the formulation, owing to local imperfections of specimens or to questionable accuracy in some regions of drawings obtained from the literature.

The frequencies here presented are compiled from lists of formulae written according to the methods customarily used in the formulation of palmar configurations in man (Cummins et al., '29), with such modifications as are necessary to adapt the method to other primates. A brief account of the scheme of formulation follows.

*Symbols for configuration types.* Formulation represents merely short-hand description, symbols being used instead of words. The basic configuration types (see fig. 596), with their descriptive symbols, are:

O, Open field — a succession of parallel ridges, straight or but gently curved, devoid of the characters which distinguish the types listed below.

V, Vestige — a local disturbance of ridge direction, such as a local rectilinear system having a direction different from the region which it adjoins, an abrupt convergence of ridges, etc. A vestige, as here formulated, has no definable relation to a particular type of true pattern (L, W or S, see below). The term vestige is not intended to imply an actual evolutionary status.

T, Tented arch — a system of ridges coursing parallel to the radiants of a triradius; ridges are abruptly reflected to form a pocket enveloping the entire length of one radiant.

L, Loop — characterized by the arrangement of ridges in looped courses, one extremity of the pattern (the "head") being thus "closed" by abruptly recurved ridges, the opposite end being "open". Types of loops are distinguished by the directions of their open extremities, indicated by superscripts, the initial letters of their directions: distal, proximal, radial, ulnar, fibular, tibial — either singly or in combinations which describe slants.

W, Whorl — a circular or elliptic figure, distinguished by concentricity of the component ridges.

S, Double-looped figure — the loops generally appearing interlocked and with their heads facing opposite directions.

In the original formulations three grades of pattern development are distinguished in loops, whorls and S-patterns. The most frequent grade in all these types is a well-developed pattern calling for no special characterization. When the construction is not quite perfected we formulate the pattern as "degenerate", and if the configuration is still more imperfect it is qualified as "vestigial". These grades of pattern expression are not distinguished in the condensed tabulations which follow. Under each of the chief pattern

types (L, W, S) the perfect, degenerate and vestigial examples are all combined.

Duplex symbols — Combinations of symbols, as individually defined above, indicate the occurrence in a single morphological area of two configurations of the types formulated.

*Symbols for regional designations.* The symbols used in designating individual configuration areas are for the most part explained by the labels of figures 3 and 4.

The following additional symbols require definition. The abbreviation H is used for the hypothenar region as a whole, applying when it is desired to combine  $H^d$  and  $H^p$  and when the two elements are not distinguishable. Central area is abbreviated to CA. The plus sign has been used to show that two adjoining morphological areas are blended in a single configuration (e.g.,  $H^d + H^p$ ;  $Th + I$ ).

**PROSIMIAE (LEMUROIDEA; PROSIMIANS)**

**DAUBENTONIIDAE**

**DAUBENTONIA (AYE-AYE)**

**TARSIIDAE**

**TARSIVUS (TARSIER)**

**NYCTICEBIDAE**

**LORIS (SLENDER LORIS)**

**NYCTICEBUS (SLOW LORIS)**

**PERODICTICUS (POTTO)**

**GALAGO (BUSH BABY)**

**LEMUR (TRUE LEMUR)**

**PROTITHECUS (SAFAKA)**

## DAUBENTONIA

## Manus (3)

## Figures 5-6

Except for a drawing in the literature (Bychowska), the dried stuffed skin of one specimen provides the only material of this genus included in the tabulation; such a preparation is obviously not ideal for examination of the dermatoglyphics. (See supplementary note, below.)

Interdigital pads I, II and III are prominent, but IV is only slightly elevated. The H pad is an expanded plateau, as is the smaller Th pad. There are faint indications of pads 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>.

The pads are only incompletely covered with continuous ridges. Small patches of ridge-bearing epidermis are distributed over parts of the pads, between and around them, and in the central area. Through these patchy areas, however, ridge directions are traceable in some areas, but with difficulty, by projection across the intervals between patches. Well formed triradii are not present, though the locations of potential triradii are recognizable as points of ridge divergence.

H: O (3). The division of two areas of ridged skin in one palm (fig. 5) suggests the distinction between H<sup>a</sup> and H<sup>p</sup>.

Th: L<sup>p</sup> (1); W (2).

I: O (3).

II: O (2); L<sup>p</sup> (1).

III: O (1); L<sup>p</sup> (2).

IV: O (3).

CA: Ridges not formed.

## Pes (2)

## Figures 7-8

The plantar pads are not as prominent as those of the hand, being even lower and having less defined outlines. Pads H and Th are not noted at all. The extent of patched areas of ridged skin is greater than in the hand. From the calcaneal



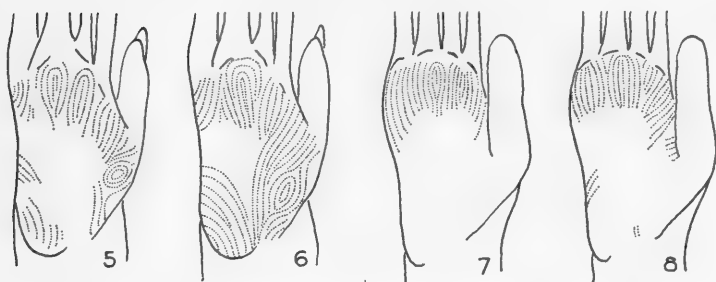
extremity as far distally as the boundary line indicated in the figures the skin is hairy. The same characteristic prevails in all the prosimians, and reference to it need not be repeated hereafter. Observations could be made only on the areas listed below, as shown in the figures.

II: O (2).

III: L<sup>p</sup> (2).

IV: O (1); questioned L<sup>p</sup> (1).

CA: Ridges not formed.



Figs. 5-6 *Daubentonia madagascariensis*, manus.

Figs. 7-8 Same, pes.

### Supplementary note

Since the completion of this work we have had opportunity to examine one hand and one foot of an adult specimen in an excellent state of preservation, loaned by Dr. A. H. Schultz (*D. madagascariensis*, Schultz's number 393). In the hand the only points of difference from the two hands here illustrated are: occurrence of islands instead of continuous ridges over the thenar region (compare variations in ridge extent in figs. 5 and 6); presence of a whorl in interdigital III (instead of open field or loop, as found in the other three hands). The plantar dermatoglyphics of this specimen do not differ in any essential from the features as drawn in figures 7 and 8. It should be noted, however, that central pads of the sole are indicated as prolongations from the related interdigital pads, separated from them by the distal transverse flexion furrow.

## TARSIUS

## Manus (8)

## Figures 9-12

The pads are prominently elevated. Pad II is the largest and most inflated of the interdigital series and pad III is the smallest in expanse. Pad IV is variable in height and extent; in one hand it is elongated and merged proximally with the H pad. Pads Th and I may be either discrete or partially merged, and in two hands H and Th are approximated and partially blended.

H<sup>d</sup> + H<sup>p</sup>: O (1); V (1); L<sup>a</sup> (1).

H<sup>d</sup>: O (2); V (3).

H<sup>p</sup>: O (1); V (4).

Th: O (2); V (2); T (2); L<sup>p</sup> (2).

I: O (8).

II: O (8).

III: O (8).

IV: O (7); V (1). Usually the open field of any one interdigital area presents a nearly parallel succession of straight ridges, though occasionally the ridges may converge slightly at the proximal border of the area.

CA: Ridges not formed.

## Pes (9)

## Figures 13-16

The typical pad arrangement is considerably modified. Only three definite prominences are expressed. One of these occupies a region proximal to digits 2, 3 and 4, extending well into the central area; this pad may be identified as a fusion of II and III. The largest prominence is U-shaped, its situation indicating that it represents the blending of IV, H and Th. There are two shallow grooves so placed as to suggest lines of juncture of these pads. Pad I is a massive elevation lying at the base of the markedly opposable hallux. In the

parathenar region the epidermis does not bear ridges, and extensions distally from it separate the prominences just described.

H (9): O (9).

C (9): Ridges not formed.

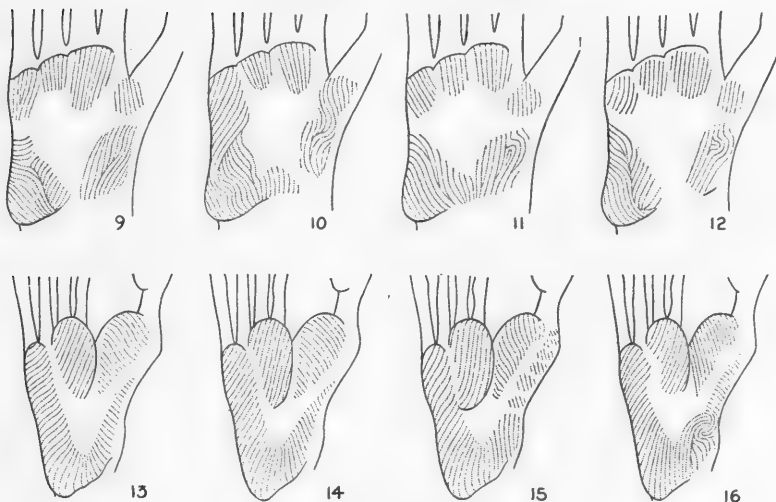
Th (9): O (7); S (2).

I (8): O (8).

II + III (8): O (8).

IV (9): O (9).

CA: Ridges not formed.



Figs. 9-12 Tarsius, manus.

Figs. 13-16 Same, pes.

#### LORIS

Pes (1) — Schlaginhaufen, figure 100

H<sup>d</sup>: L<sup>p</sup>.

H<sup>p</sup>: W.

C: Ridges not formed.

Th: V.

I: W.

II: O.

III: O.

IV: O.

CA: Ridge disturbance (3<sup>p</sup>); otherwise this area presents a lack of ridge formation.

## NYCTICEBUS

## Manus

## Figures 17-20

There are six well-defined border pads, the most prominent being I, II and H, and the smallest, III. The broad base of the highly opposable pollex bears the greater part of pad I and a portion of Th.

Pads 2<sup>p</sup> and 3<sup>p</sup> are small but definite in one hand of the single individual examined in this respect, absent in the other. The epidermis is continuously ridged except in a relatively small part of the central area and in the flexion furrows.

(H, 8) H<sup>d</sup> + H<sup>p</sup>: O (1); L<sup>d</sup> (1); W (1); S (3).

H<sup>d</sup>: L<sup>u</sup> (1); W (1).

H<sup>p</sup>: O (1); V (1).

Th (7): O (3); V (2); L<sup>d</sup> (2).

I (7): W (5); S (1); L<sup>d</sup>W (1).

II (8): W (5); S (3).

III (8): O (3); V (1); L<sup>p</sup> (1); W (3).

IV (7): O (2); V (1); L<sup>p</sup> (2); W (2).

IV<sup>u</sup> (7): O (1); L<sup>d</sup> (1); L<sup>p</sup> (3); W (2).

CA (8): O (6). 2<sup>p</sup>: L<sup>r</sup> (1).

3<sup>p</sup> and 4<sup>p</sup>: V and V (1).

## Pes

## Figures 21-24

The pads are not only prominently elevated but they are also outlined by flexion furrows. Some are crossed by flexion furrows, but the unity of a pad thus subdivided is reflected in the singleness of its configuration. The base of the hallux bears I and Th, fused in a single eminence. The hypothenar region bears two separate prominences, H<sup>d</sup> and H<sup>p</sup>. In both soles of one animal central pads occur, 2<sup>p</sup> and 3<sup>p</sup>.

(H, 7)  $H^d + H^p$ :  $L^t$  (1).

$H^d$ : V (1);  $L^d$  (1); W (4).

$H^p$ : O (6).

C (7): This region is hairy.

Th (7): O (7).

I (7): W (5); S (1);  $WL^d$  (1).

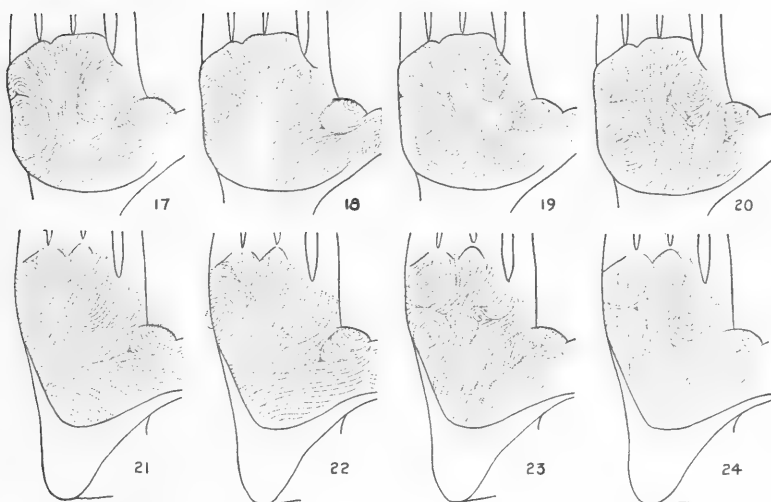
II (7): O (2);  $L^d$  (2); W (2); S (1).

III (7): O (7).

IV (7): O (7).

$IV^t$  (6): O (1);  $L^d$  (1);  $L^p$  (1); W (2); S (1).

CA: In each of the four soles in our original material local features of the central area are noted:  $2^p$ :  $L^t$  (1).  $2^p$  and  $3^p$ : V and V (1). The absence of local features in this area in three soles illustrated in the literature (Kidd, Schlaginhaufen, Alix) should not be regarded as evidence of their actual lack, since such disturbances might have been considered insignificant by these authors.



Figs. 17-20 *Nycticebus borneanus*, manus.

Figs. 21-24 Same, pes.

## PERODICTICUS

## Manus (2)

## Figures 25-26

The palmar reliefs resemble in a general way those in *Nycticebus*. As in the latter, the pollex is highly opposable and its base bears large portions of the massive pads I and Th. The other pads of the border series (II, III, IV and H) occur in their typical locations. A pad not belonging to the basic plan (a secondary pad, Whipple—indicated by the patterns shown in figs. 25-26) is found on the proximal phalanx of the pollex.

The entire palmar surface presents minute spots of brownish-black pigmentation, especially concentrated over the pads. With the aid of a loupe it is noted that the pigment is deeply seated. In the central area the spots are rounded, but over the pads they are elongated in line with the epidermal ridges.

H<sup>d</sup>: W (2).  
 H<sup>p</sup>: O (2).  
 Th: L<sup>p</sup> (2).  
 I: W (1); WL<sup>d</sup> (1).  
 II: L<sup>d</sup> (2).  
 III: O (2).  
 IV: O (1); V (1).  
 CA: Ridges not formed.

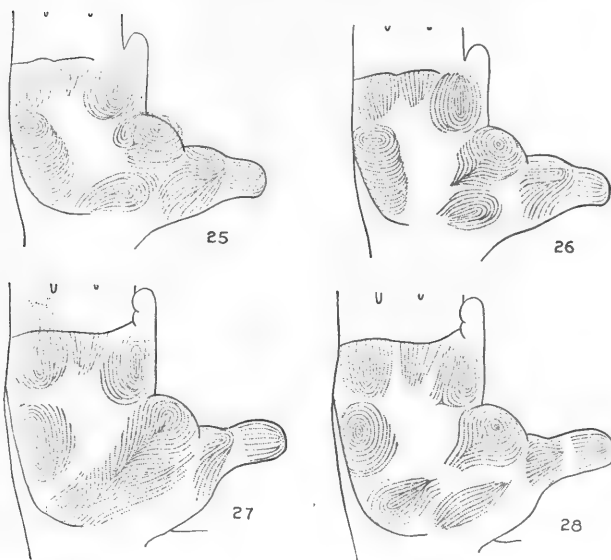
## Pes

## Figures 27-28

The pads are quite similar to those of the hand, the only noteworthy difference being a partial division of Th into tibial and fibular components. Pigmentation corresponds to that of the palm, though the pigmented areas are hardly as numerous.

H<sup>d</sup>: W (2).  
 H<sup>p</sup>: L<sup>t</sup> (2).  
 C: Ridges not formed.  
 Th: O (2).  
 I: W (2).  
 II: L<sup>d</sup> (1); W (1).

III: O (2).  
 IV: L<sup>d</sup> (2).  
 CA: Ridges not formed.



Figs. 25-26 *Perodicticus potto*, manus.

Figs. 27-28 Same, pes.

#### GALAGO

##### Manus

##### Figures 29-30

The six typical pads of the border region are prominent and massive, Th being the smallest. Only the summits and a part of the descending slopes of the pads are ridge-bearing. Immediately adjoining these areas there are small patches of ridged skin, and elsewhere only islands occur. The same conditions obtain in the sole.

(H, 4) H<sup>d</sup> + H<sup>p</sup>: W (2); S (1).  
 H<sup>d</sup>: W (1).  
 H<sup>p</sup>: L<sup>d</sup> (1).  
 Th (4): W (4).

I (4): W (1); VW (1); S (1); SW (1).

II (4): W (3); SV (1).

III (3): W (3).

IV (3): W (1); S (2).

[One of the hands is that of *Hemigalago*, figured by Whipple. In it the hypothenar area bears a single whorl, and since all other areas bear whorls the figures above may be easily adjusted if it is desired to exclude this specimen.]

CA: Ridges not formed.

Pes (4)

Figures 31-32

The pad arrangement corresponds very closely to that of the palm, with only the following differences: one of the two feet lacks the Th pad; 2<sup>p</sup> is present in both soles.

(H, 4) H<sup>d</sup> + H<sup>p</sup>: W (1).

H<sup>d</sup>: W (3).

H<sup>p</sup>: No ridges formed.

C: No ridges formed.

Th: L<sup>p</sup> (1); W (2); no ridges formed (1).

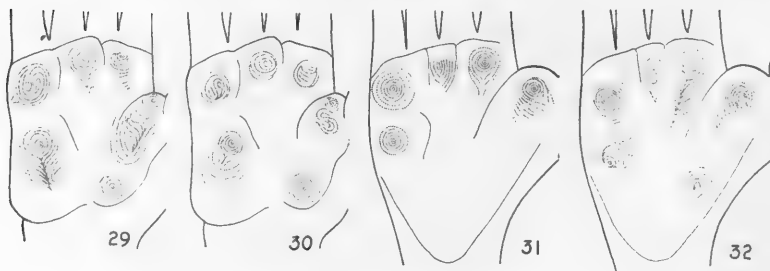
I: L<sup>p</sup> (1); L<sup>t</sup> (1); W (2).

II: W (3); S (1).

III: L<sup>d</sup> (2); W (2).

IV: L<sup>d</sup> (1); W (3).

CA: Ridges not formed.



Figs. 29-30 *Galago zuluensis*, manus.

Figs. 31-32 Same, pes.



## LEMUR

## Manus

## Figures 33-36

There are but five pads of the border series instead of the typical six, the reduction in number being apparently due to fusion of Th and I. Pad H is constricted transversely, H<sup>d</sup> and H<sup>p</sup> being thus separated. The pads are not markedly elevated. A distinctive feature of the palm is the presence of numerous patches of ridge-bearing skin, ranging in diameter up to several millimeters, intermingled with much more minute "epidermal rings" (Whipple). It is of interest to note that three patches of ridged skin, larger than those found in any other area, occur in the positions 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>. Notwithstanding the discontinuity of ridged skin, the general courses of ridges follow common directions, hence admitting tracings such as those shown in the figures.

(H, 13) H<sup>d</sup>: O (9); L<sup>u</sup> (2); L<sup>r</sup> (1); W (1).

H<sup>p</sup>: L<sup>u</sup> (11); W (2).

(Th, 10) Th + I: O (1); L<sup>d</sup> (1); S (2).

Th: O (1); V (1); L<sup>d</sup> (2); L<sup>r</sup> (2).

(I, 10) I + Th: See above.

I: O (3); V (1); L<sup>p</sup> (1); W (1).

II (12): L<sup>r</sup> (2); W (7); S (3).

III (11): L<sup>d</sup> (6); W (5).

IV (9): L<sup>d</sup> (1); W (8).

CA (13): O (13).

## Pes

## Figures 37-40

As in the palm, pads are somewhat flattened. The same series of border pads is recognizable, with a suggestion of separation of H<sup>d</sup> and H<sup>p</sup>, and a distinct division of Th<sup>d</sup> and Th<sup>p</sup>.

The central area corresponds to that of the palm in presenting a mingling of ridged patches and epidermal rings. In several soles this condition extends even into the territories of border pads, involving particularly H and Th.

(H, 14)  $H^d + H^p$ : O (9);  $L^d$  (1).

$H^d$ : V (2);  $L^t$  (2).

$H^p$ : O (2);  $L^d$  (2).

C (15): Hairy throughout with the exception of one foot illustrated by Kidd, which presents a bare area at the extremity of the heel.

Th (14): O (11); V (1);  $L^t$  (1);  $L^t L^t$  (1).

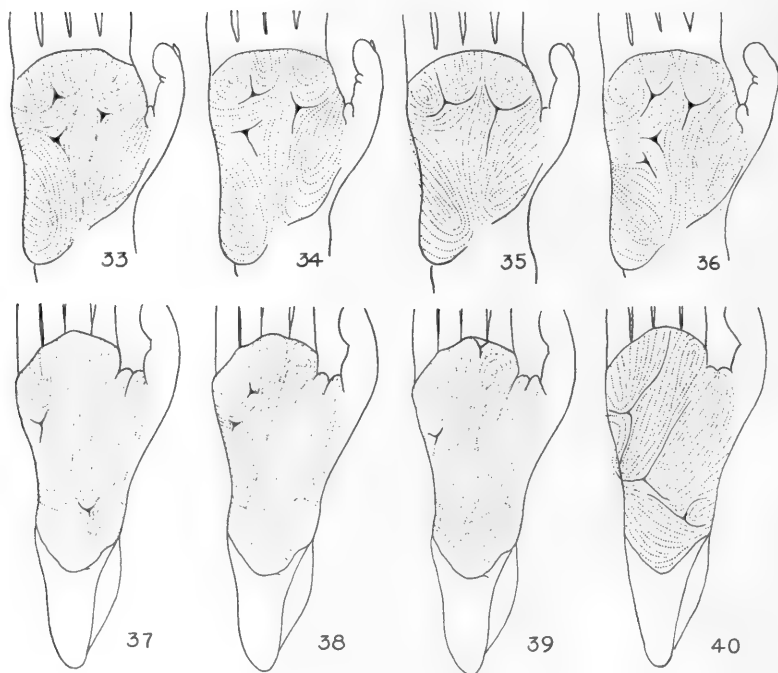
I (13): O (9); V (1);  $L^p$  (3).

II (12): O (2); V (1);  $L^t$  (1);  $L^p$  (4); W (3); S (1).

III (11): O (3);  $L^d$  (1);  $L^p$  (3); W (3); S (1).

IV (11): O (1); V (1);  $L^d$  (8); W (1).

CA (15): O (13);  $L^d$  (2).



Figs. 33-36 *Lemur variegatus*, manus.

Figs. 37-40 Same, pes.

## PROPITHECUS

Manus (1) — Bychowska, figure 4

H: O.

Th + I: L<sup>d</sup>. In I the ridge-bearing area is represented by small patches.

II + III: L<sup>p</sup>.

IV: O.

CA: O.

SIMIAE (ANTHROPOIDEA; SIMIANS)

PLATYRRHINAE (NEW WORLD MONKEYS)

CALLITHRICHIDAE (MARMOSET-LIKE MONKEYS)

SENIOCEBUS (BALD-HEADED TAMARIN)

LEONTOCEBUS (TAMARIN)

OEDIPOMIDAS (MARMOSET)

CALLITHRIX (TRUE MARMOSET)

## SENIOCEBUS

## Manus (2)

## Figures 41-42

The palm, as in other genera of Callithrichidae examined, is generally flattened; while their outlines are distinct, the pads are but little bulged. Pad H is clearly divided into H<sup>a</sup> and H<sup>p</sup>, the latter being the most prominently elevated of all the pads. Th and I are combined to form an elongated eminence, though the two elements are distinguishable. Pads 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup> are small; on them, as a rule, and in the neighboring central area ridges are incompletely formed.

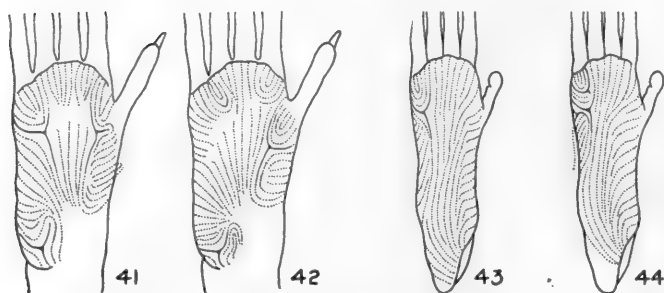
H<sup>a</sup>: O (2).  
H<sup>p</sup>: T (2).  
Th: L<sup>p</sup> (1); W (1).  
I: L<sup>a</sup> (2).  
II: L<sup>a</sup> (2).  
III: O (1); L<sup>a</sup> (1).  
IV: L<sup>a</sup> (2).  
CA: O (2).

## Pes (2)

## Figures 43-44

As in other Callithrichidae, the sole of *Seniocebus* presents the usual border pads, which are generally flattened. Pads Th and I form a single elevation, and H is elongated. Pad II is divided by a flexion fold (the simian line). Pads 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup> occur, 2<sup>p</sup> being the largest.

H<sup>a</sup>: L<sup>p</sup> (2).  
H<sup>p</sup>: O (2).  
C: O (2).  
Th: O (2).  
I: O (2).  
II: O (2).  
III: O (2).  
IV: L<sup>a</sup> (2).  
CA: O (2).

Figs. 41-42 *Seniocebus bicolor*, manus.

Figs. 43-44 Same, pes.

## LEONTOCEBUS

## Manus (3)

## Figures 45-46

H<sup>d</sup>: O (2); L<sup>p</sup> (1).H<sup>p</sup>: L<sup>a</sup> (3).Th: L<sup>r</sup> (1); W (2).

I: O (1); W (1); S (1).

II: O (1); L<sup>d</sup> (2).

III: O (2); V (1).

IV: O (1); L<sup>d</sup> (1); W (1).

CA: Ridges incompletely formed.

## Pes (2)

## Figures 47-48

H<sup>d</sup>: L<sup>f</sup> (2).H<sup>p</sup>: V (2).

C: O (2).

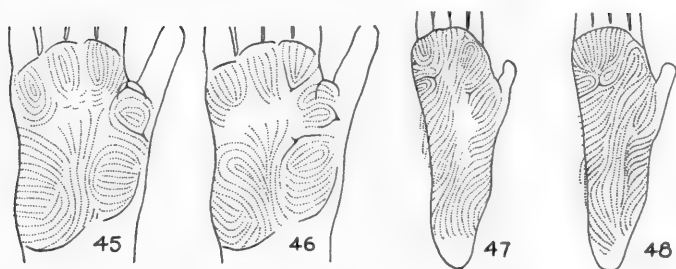
Th: O (1); V (1).

I: O (2).

II: L<sup>p</sup> (2).

III: O (2).

IV: L<sup>d</sup> (2).CA: 3<sup>p</sup>: L<sup>d</sup> (1). 4<sup>p</sup>: L<sup>f</sup> (1). Elsewhere there are open fields or deficient ridges.

Figs. 45-46 *Lentocebus*, manus.

Figs. 47-48 Same, pes.

## OEDIPOMIDAS

## Manus

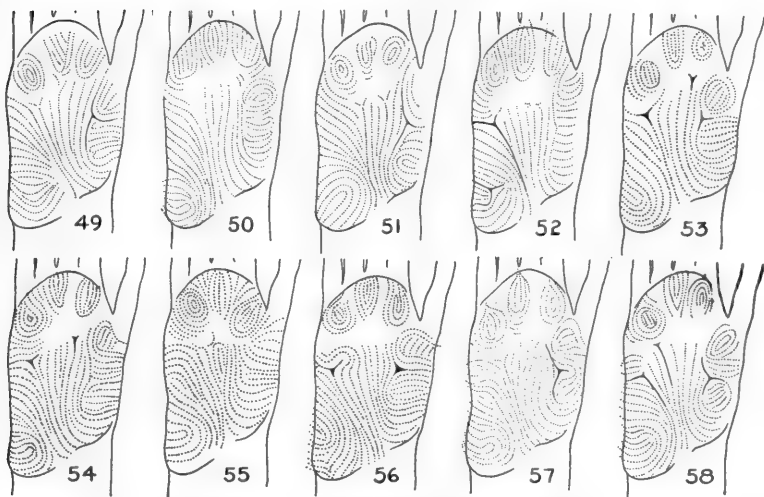
## Figures 49-58

(H, 14)  $H^d + H^p$ : S (1). $H^d$ : O (8); T (4);  $L^r$  (1). $H^p$ :  $L^u$  (12); S (1).

(Th, 13) Th + I: S (1).

Th: V (2); T (1);  $L^r$  (7); W (2).

(I, 13) I + Th: See above.

I: O (1); V (3);  $L^d$  (2); W (6).II (13):  $L^d$  (6); W (7).Figs. 49-58 *Oedipomidas geoffroyi*, manus.

III (13): V (3); L<sup>d</sup> (7); L<sup>p</sup> (1); W (2).

IV (13): V (1); W (12).

CA (14): 3<sup>p</sup>: L<sup>p</sup> (1). Elsewhere in this hand and throughout in all others there are open fields or deficient ridges.

### Pes

#### Figures 59-68

(H, 14) H<sup>d</sup>: V (4); L<sup>f</sup> (7); W (3).

H<sup>p</sup>: O (14).

C (13): O (13).

(Th, 13) Th + I: V (2); L<sup>f</sup>L<sup>f</sup> (1).

Th: O (5); V (4); W (1).

(I, 13) I + Th: See above.

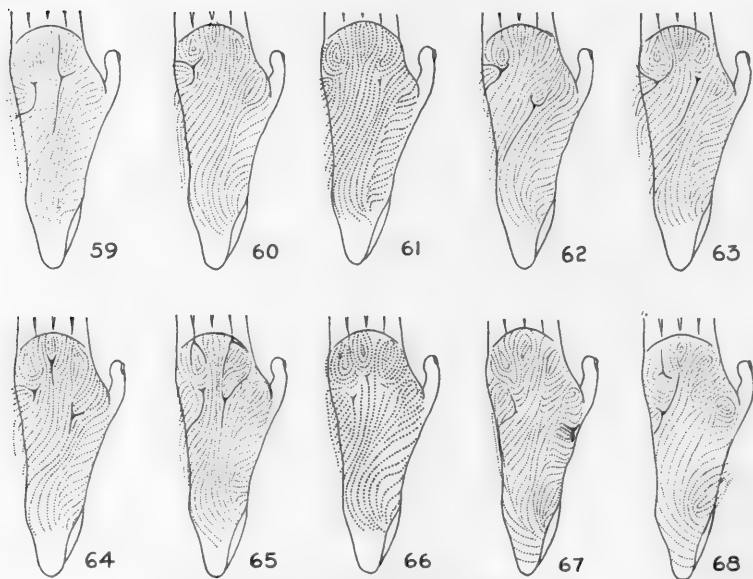
I: O (1); V (2); L<sup>d</sup> (1); L<sup>p</sup> (4); W (2).

II (14): O (1); V (2); L<sup>p</sup> (5); W (5); VW (1).

III (14): O (3); V (4); L<sup>d</sup> (3); L<sup>p</sup> (1); W (3).

IV (13): T (1); L<sup>d</sup> (6); W (6).

CA (13): O (5). 2<sup>p</sup>: V (1); L<sup>d</sup> (6). 2<sup>p</sup> and 4<sup>p</sup>: V and V (1).



Figs. 59-68 *Oedipomidas geoffroyi*, pes.



## CALLITHRIX

## Manus

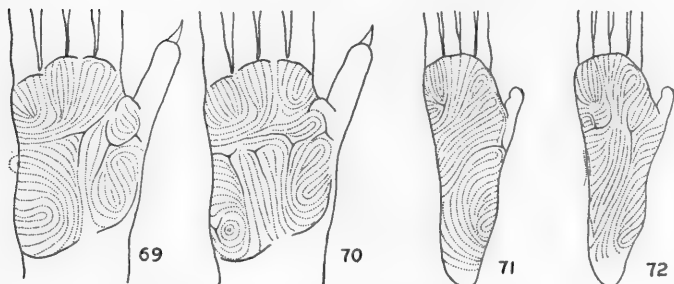
## Figures 69-70

- (H, 5)  $H^d$ : O (4);  $L^r$  (1).  
 $H^p$ :  $L^u$  (4); W (1).  
 (Th, 5) Th + I: O (1).  
 Th: O (1); S (3).  
 (I, 5) I + Th: See above.  
 I:  $L^d$  (2);  $L^u$  (2).  
 II (4):  $L^d$  (2);  $L^p$  (1);  $L^u$  (1).  
 III (4): O (2);  $L^d$  (1);  $L^p$  (1).  
 IV (4): T (1);  $L^u$  (2); W (1).  
 CA (4): O (1).  $2^p$  and  $3^p$ : V and V (1).  
 $2^p$ ,  $3^p$ , and  $4^p$ : V, V, and V (1).  
 $3^p$  and  $4^p$ :  $L^p$  and  $L^p$  (1).

## Pes (5)

## Figures 71-72

- $H^d$ : O (1);  $L^p$  (3); W (1).  
 $H^p$ : O (4); V (1).  
 C: O (4);  $L^d$  (1).  
 Th: O (1); V (1);  $L^t$  (1);  $L^t L^f$  (2).  
 I: O (1);  $L^d$  (1);  $L^f$  (1);  $L^p$  (2).  
 II: O (1);  $L^f$  (1);  $L^p$  (3).  
 III: O (5).  
 IV:  $L^d$  (4); W (1).  
 CA: O (2).  $4^p$ : V (3).

Figs. 69-70 *Callithrix jacchus*, manus.

Figs. 71-72 Same, pes.

SIMIAE (ANTHROPOIDEA; SIMIANS)

PLATYRRHINAE (NEW WORLD MONKEYS)

CEBIDAE (CAPUCHIN-LIKE MONKEYS)

ALOUATTA (HOWLER)

SAIMIRI (SQUIRREL MONKEY)

AOTUS (DOUROUCOULI; NIGHT MONKEY)

ATELES (SPIDER MONKEY)

LAGOTHRIX (WOOLLY MONKEY)

CEBUS (CAPUCHIN)

## ALOUATTA

## Manus

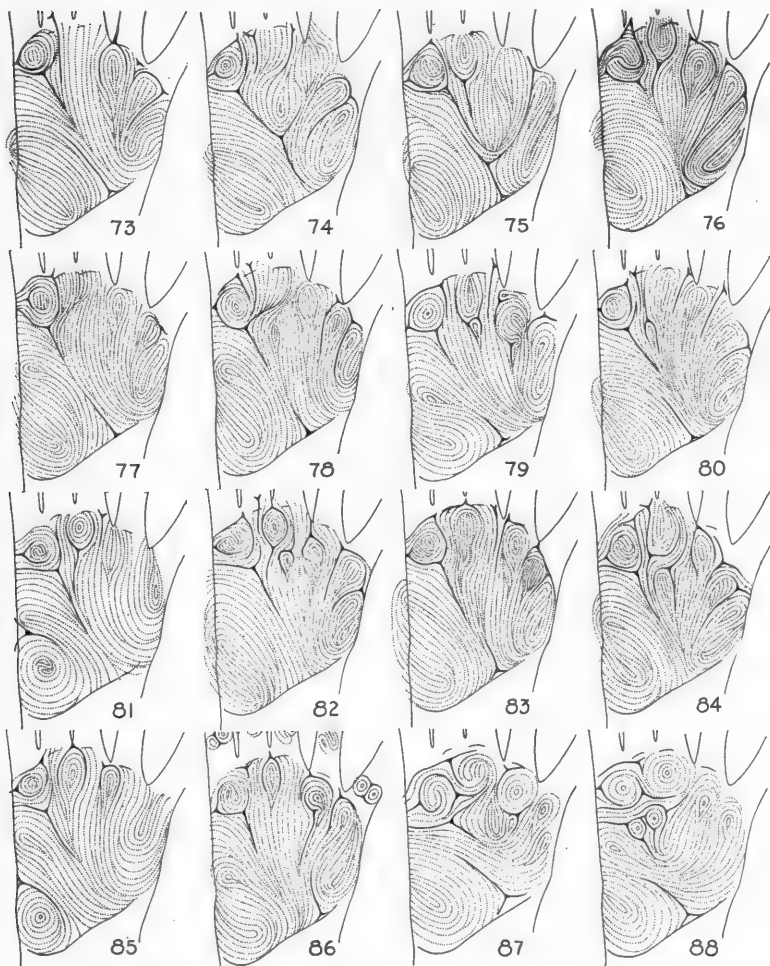
## Figures 73-88

All border pads of the basic plan are present. Pad Th is small. Pads 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup> are evident.

(H, 19) H<sup>d</sup> + H<sup>p</sup>: S (14).

H<sup>d</sup>: O (1); L<sup>p</sup> (3); L<sup>r</sup> (1).

H<sup>p</sup>: L<sup>u</sup> (3); W (1); S (1).



Figs. 73-88 Alouatta, manus.

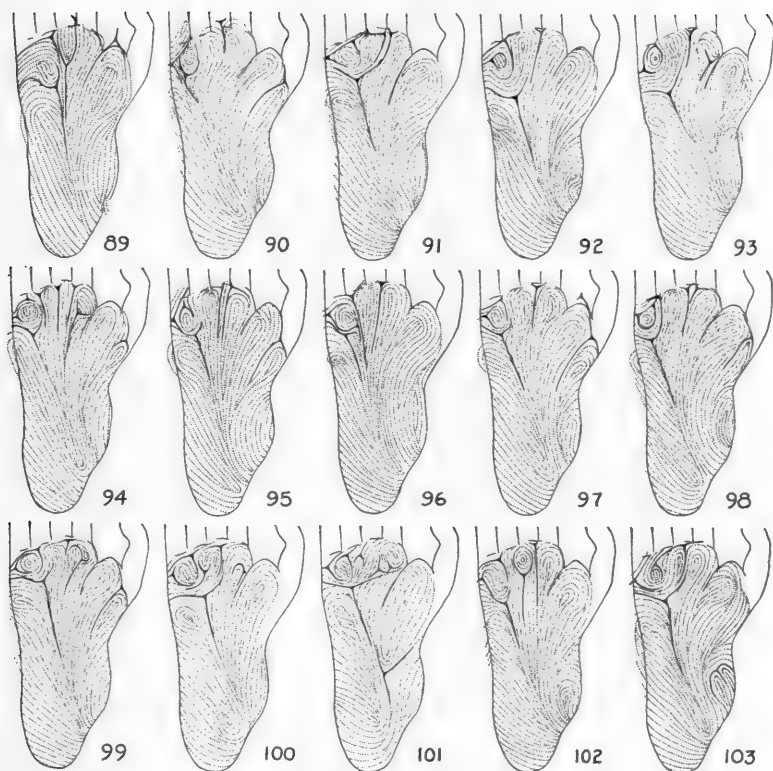
- (Th, 18) Th + I: L<sup>p</sup> (1); W (1); S (3).  
 Th: O (2); L<sup>p</sup> (1); W (3); S (7).  
 (I, 18) I + Th: See above.  
 I: L<sup>d</sup> (2); L<sup>p</sup> (10); W (1).  
 II (18): O (1); V (1); L<sup>d</sup> (1); L<sup>p</sup> (14); W (1).  
 III (18): O (3); V (1); L<sup>d</sup> (4); L<sup>p</sup> (3); W (5); S (2).  
 IV (18): W (13); S (5).  
 CA (18): O (4). 2<sup>p</sup>: T (1); S (1).  
     3<sup>p</sup>: L<sup>p</sup> (1). 4<sup>p</sup>: V (1).  
     2<sup>p</sup> and 3<sup>p</sup>: V and L<sup>p</sup> (1); T and  
     L<sup>p</sup> (1). Between 3<sup>p</sup> and 4<sup>p</sup>: V (1);  
     L<sup>p</sup> (1). 3<sup>p</sup> and 4<sup>p</sup>: W and W (1).  
     2<sup>p</sup> + 3<sup>p</sup> and 4<sup>p</sup>: V and V (2); V and  
     L<sup>p</sup> (1). 2<sup>p</sup> and 3<sup>p</sup> + 4<sup>p</sup>: V and V (1).  
     P-th: L<sup>d</sup> (3, two of these occurring in  
     hands which have also distal features).

## Pes (22)

### Figures 89-103

Border pads and pads of the distal part of the central area conform to the usual arrangement, but it may be noted especially that Th<sup>d</sup> and Th<sup>p</sup> are far separated, the former being placed in close relationship to the very conspicuous I:

- H<sup>d</sup> + H<sup>p</sup>: L<sup>p</sup> (3).  
 H<sup>d</sup>: L<sup>p</sup> (18); W (1).  
 H<sup>p</sup>: O (18); L<sup>p</sup> (1).  
 C: O (5); L<sup>d</sup> (17).  
 Th<sup>p</sup>: O (10); V (2); L<sup>p</sup> (9); L<sup>p</sup>L<sup>p</sup> (1).  
 Th<sup>d</sup>: O (11); V (2); L<sup>p</sup> (9).  
 I: L<sup>d</sup> (1); L<sup>p</sup> (21).  
 II: O (1); L<sup>p</sup> (17); W (1); S (3).  
 III: O (3); V (1); L<sup>d</sup> (1); L<sup>p</sup> (14); W (1); S (2).  
 IV: L<sup>d</sup> (2); W (12); S (7); L<sup>d</sup>W (1).  
 CA: O (18). 4<sup>p</sup>: V (1); L<sup>p</sup> (2). P-th: L<sup>d</sup> (1).

Figs. 89-103 *Alouatta*, pes.

## SAIMIRI

## Manus

## Figures 104-115

The expanded H pad shows no indication of subdivision into  $H^d$  and  $H^p$ , and the Th pad is absorbed with I into a single large eminence with its summit in the area of I.

(H, 21)  $H^d + H^p$ :  $L^u$  (13); W (3); S (3).

$H^d$ : V (1); T (1).

$H^p$ : T (1);  $L^u$  (1).

(Th, 21) Th + I:  $L^d$  (1).

Th: O (16);  $L^r$  (2); W (1); S (1).

(I, 21) I + Th: See above.

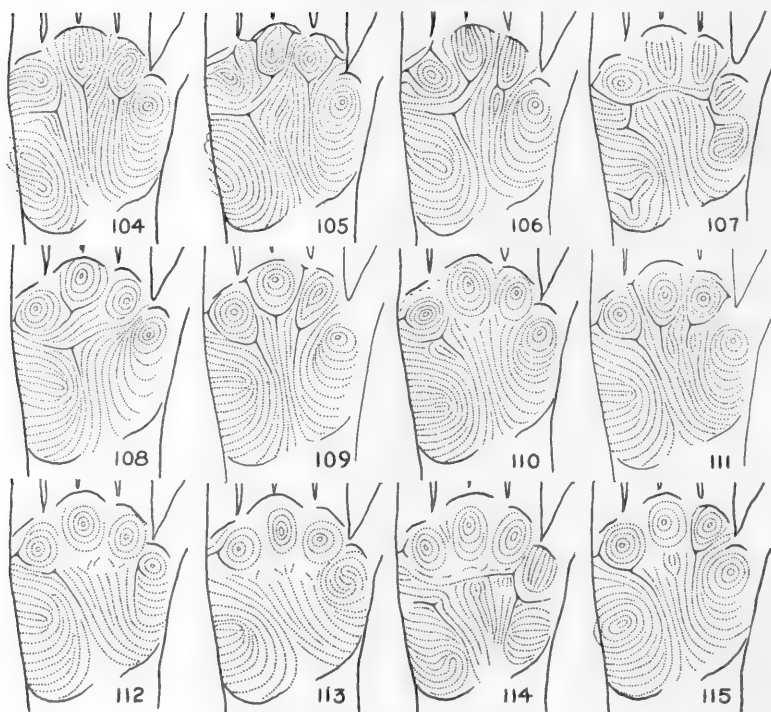
I: V (1); L<sup>d</sup> (2); W (16); S (1).

II (21): L<sup>d</sup> (4); L<sup>p</sup> (1); W (16).

III (21): V (1); L<sup>d</sup> (4); W (16).

IV (21): L<sup>v</sup> (2); W (18); S (1).

CA (20): 2<sup>p</sup>: L<sup>p</sup> (1). 3<sup>p</sup>: V (1). 4<sup>p</sup>: V (2); L<sup>p</sup> (2). 2<sup>p</sup> and 3<sup>p</sup>: V and V (1). 3<sup>p</sup> and 4<sup>p</sup>: V and V (1). 2<sup>p</sup>, 3<sup>p</sup>, and 4<sup>p</sup>: V, V, and V (3). 2<sup>p</sup> + 3<sup>p</sup> + 4<sup>p</sup>: a broad vestigial L<sup>p</sup> (2). The distal portion of the central area of the remaining seven soles is in part lacking in formed ridges, though there is an evident tendency toward the expression of local irregularities conforming in position to 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>.

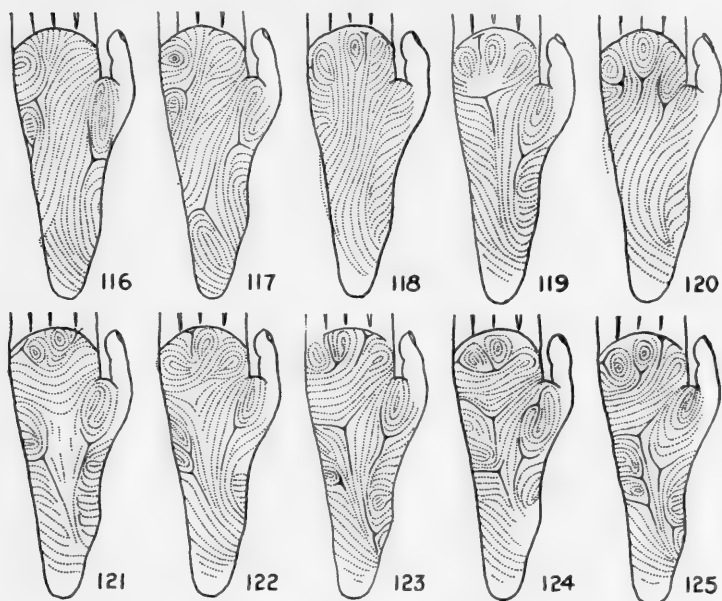


Figs. 104-115 Saimiri, manus.

## Pes

## Figures 116-125

- (H, 21)  $H^d + H^p$ : V (2);  $L^f$  (1); W (1); S (4).  
 $H^d$ : O (5); V (1);  $L^f$  (2); W (4); S (1).  
 $H^p$ : O (10);  $L^f$  (1); S (2).  
C (21): O (17);  $L^f$  (1);  $L^p$  (3).  
Th (21): O (2); V (5);  $L^p$  (1);  $L^t$  (11); W (2).  
I (21): O (1); V (1);  $L^d$  (6);  $L^p$  (1);  $L^t$  (1); S (10);  
TL<sup>p</sup> (1).  
II (20): O (3); V (2);  $L^f$  (10);  $L^p$  (4); S (1).  
III (21): O (4); V (1);  $L^p$  (8); W (8).  
IV (21):  $L^f$  (3);  $L^t$  (3); W (14); S (1).  
CA (21): O (21).



Figs. 116-125 Saimiri, pes.

## AOTUS

Photographs of the hand and foot of *Aotus* are illustrated in figures 1 and 2. The conspicuous border and central pads are located in agreement with the dermatoglyphic plan shown in figures 3 and 4. The occurrence of II<sup>t</sup> and IV<sup>u</sup> should be specially noted as additions to the regular series of the distal border pads.

## Manus (13)

## Figures 126-137

H<sup>d</sup>: O (13).

H<sup>p</sup>: O (4); V (8); L<sup>u</sup> (1).

(In two hands there are slight shiftings of  
H<sup>p</sup> vestiges to a level suggesting H<sup>d</sup> + H<sup>p</sup>.)

Th + I: W (1).

Th: O (4); V (1); L<sup>r</sup> (6); W (1).

I + Th: See above.

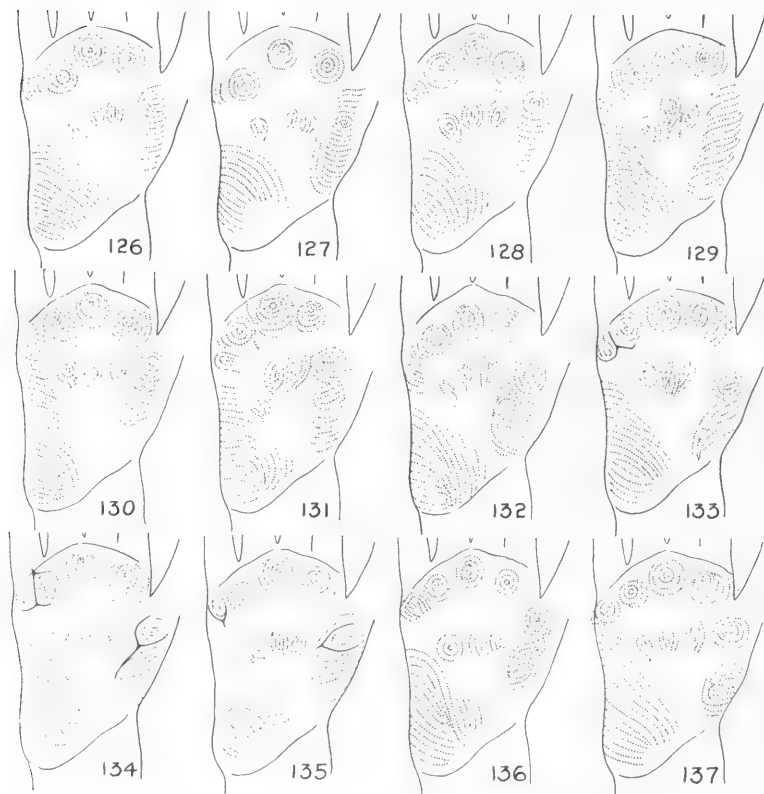
I: O (1); W (11).

II<sup>r</sup>: V (1); No ridge formation (12).

II: W (13).

III: W (13).

IV: W (13).



Figs. 126-137 *Aotus zonalis*, manus.

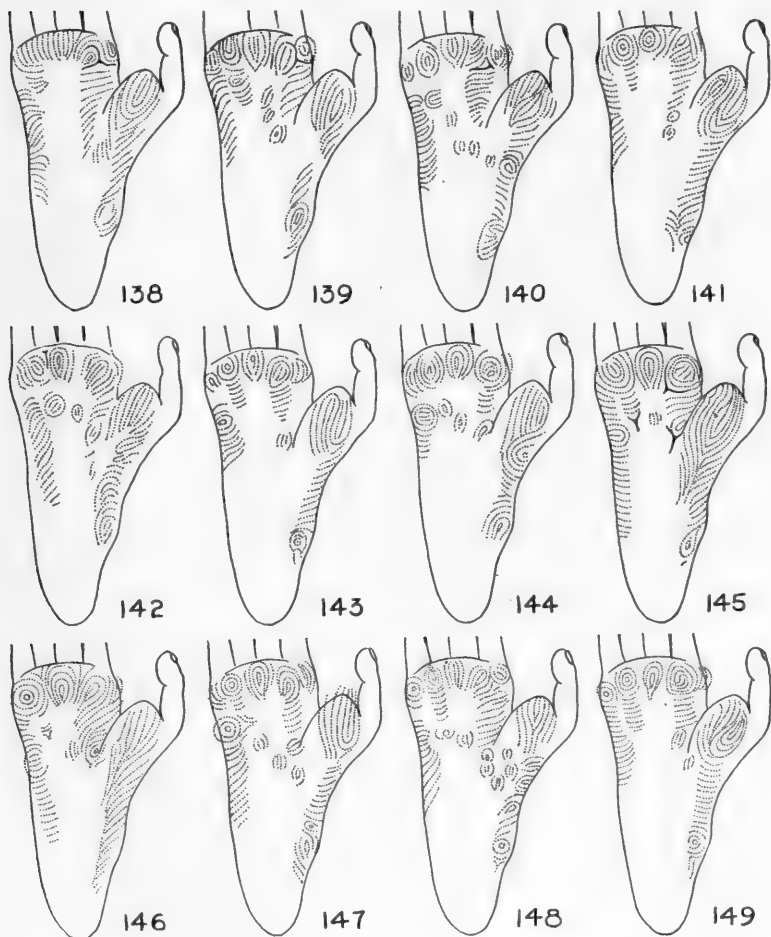


IV<sup>a</sup>: O (1); V (5); L<sup>d</sup> (2); L<sup>p</sup> (1); L<sup>r</sup> (2); W (2).  
 CA: 2<sup>p</sup>, 3<sup>p</sup>, and 4<sup>p</sup>: V, V, and V (5); V, V, and  
 L<sup>p</sup> (1); V, V, and W (2); V, L<sup>p</sup>, and L<sup>p</sup> (1);  
 L<sup>p</sup>, V, and W (1); L<sup>p</sup>, L<sup>p</sup>, and L<sup>p</sup> (3).

## Pes

## Figures 138-149

(H, 13) H<sup>a</sup>: O (7); V (1); W (5).  
 H<sup>p</sup>: O (6); No ridge formation (7).  
 C (13): No ridge formation.



Figs. 138-149 *Aotus zonalis*, pes.

Th (13): Th<sup>p</sup>: O (1); V (3); L<sup>p</sup> (3); L<sup>t</sup> (1); W (5).  
 Th<sup>d</sup>: O (10); V (2); L<sup>t</sup> (1).

I (12): V (2); L<sup>d</sup> (5); S (5).

(II<sup>t</sup>, 12) II<sup>t</sup> + II: W (2).

II<sup>t</sup>: O (1); V (5); L<sup>d</sup> (1); W (3).

(II, 13) II + II<sup>t</sup>: See above.

II: O (1); V (3); L<sup>p</sup> (5); W (1); S (1).

III (13): O (1); V (1); L<sup>d</sup> (1); L<sup>p</sup> (6); W (4).

(IV, 13) IV + IV<sup>t</sup>: V (1); W (1).

IV: V (1); L<sup>d</sup> (2); W (8).

(IV<sup>t</sup>, 13) IV<sup>t</sup> + IV: See above.

IV<sup>t</sup>: O (3); V (5); L<sup>p</sup> (1); W (2).

CA (13): 2<sup>p</sup>: VV (3); L<sup>p</sup> (1). 2<sup>p</sup> and 4<sup>p</sup>: V and  
 W (1); L<sup>d</sup>V and V (1). 2<sup>p</sup>, 3<sup>p</sup>, and 4<sup>p</sup>:  
 V, V, and V (6); W, V, and V (1).

#### ATELES

##### Manus

#### Figures 150-169

Even with the absence of the pollex and the elongation of the hand, the spatial relationships of border pads remain unchanged. The palm as a whole and the individual pads are flattened, H<sup>p</sup> being the most elevated. Central pads when expressed at all are but faintly evident.

(H, 45) H<sup>d</sup>: O (8); L<sup>pr</sup> (35); W (2).

H<sup>p</sup>: L<sup>du</sup> (34); W (6); S (5).

(Th, 42) Th + I: O (10).

Th: O (18); V (6); L<sup>r</sup> (8).

(I, 42) I + Th: See above.

I: O (6); V (5); L<sup>pu</sup> (21).

II (48): O (2); V (7); L<sup>d</sup> (36); W (3).

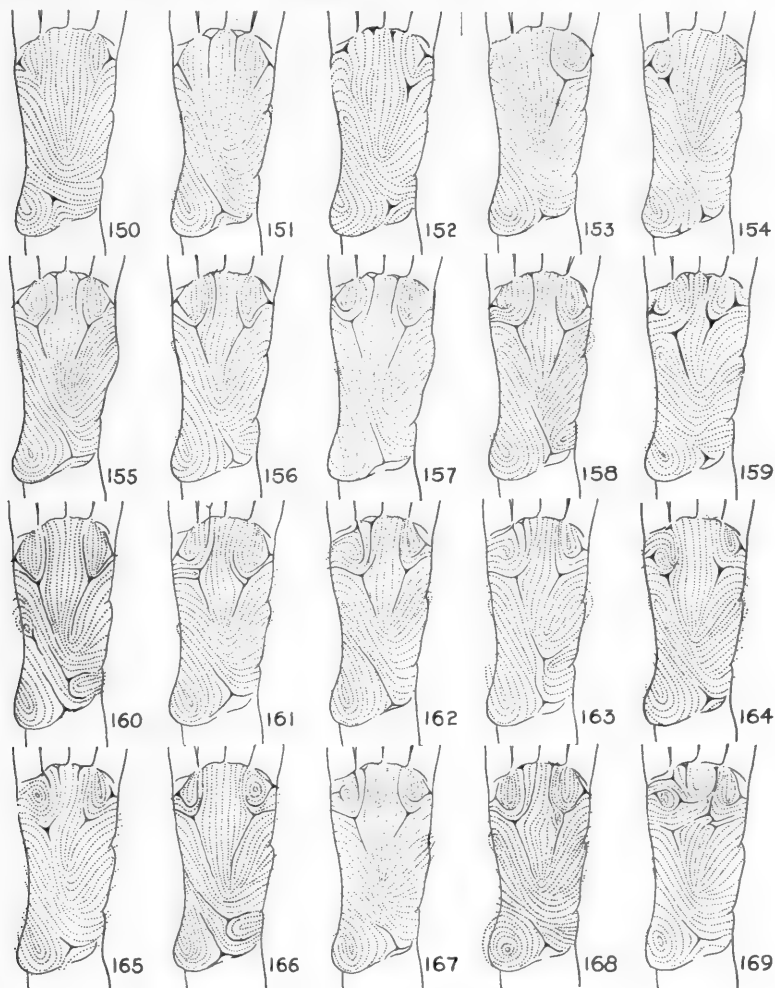
III (49): O (46); L<sup>d</sup> (3).

IV (48): O (4); V (3); L<sup>d</sup> (28); L<sup>u</sup> (2);  
 W (6); S (5).

CA (42): The central area is consistent in its general appearance, though variable in detailed configuration. As will be noted in the illustrations (figs. 150-169), the radiants

extended from triradii associated with areas II and IV form boundaries of a centrally located rhomboidal field. It is in the parathenar region where the variability is chiefly expressed, the occurrence or lack of a loop head in this area or the formation of a tented arch being

the main point of interest. The head of an  $L^d$  or a tented arch occurs in 39 palms. Three palms are open fields in both P-th and distal central area; the remaining three have distal features additional to P-th.  $2^p$ : V (1);  $L^pV$  (1).  $2^p$  and  $4^p$ :  $L^d$  and  $L^u$  (1).

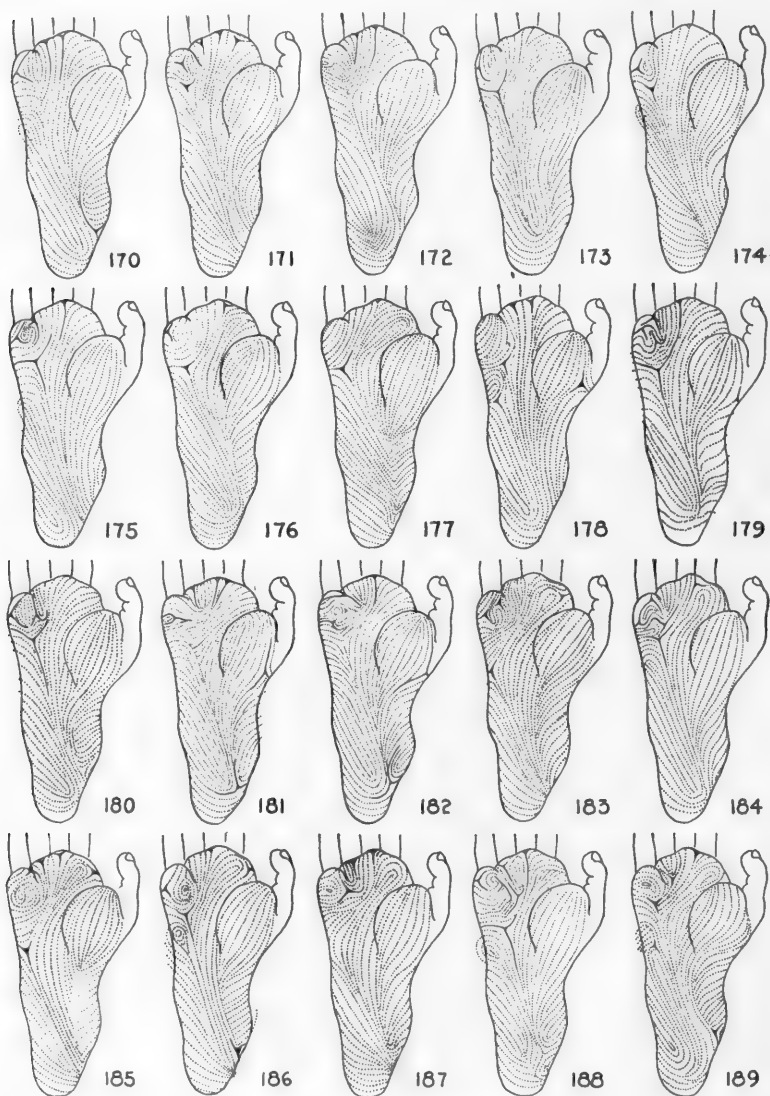


Figs. 150-169 *Ateles*, manus.

## Pes

## Figures 170-189

Individual pads, as well as the surface of the planta as a whole, are flattened, pad I being the most marked.



Figs. 170-189 *Ateles*, pes.

(H, 34)  $H^d + H^p$ :  $L^p$  (1).

$H^d$ : O (17); V (1);  $L^t$  (1);  $L^p$  (12); W (1); S (1).

$H^p$ : O (33).

C (34): O (9); V (1);  $L^{dt}$  (24).

Th (34): O (16); V (7);  $L^t$  (10); W (1).

I (34): O (31); V (1);  $L^p$  (2).

II (34): O (18); V (4);  $L^p$  (12).

III (34): O (26); V (3);  $L^d$  (4); W (1).

IV (33): O (3); V (2); T (2);  $L^d$  (5); W (2); S (19).

CA (34): O (26).  $4^p$ : V (1). P-th:  $L^d$  (7).

#### LAGOTHRIX

##### Manus (6)

##### Figures 190-193

The border pads and central pads are of the usual number and arrangement.

$H^d$ : T (1);  $L^p$  (3);  $L^u$  (2).

$H^p$ :  $L^u$  (5); S (1).

Th + I: O (1).

Th: O (3);  $L^d$  (2).

I + Th: See above.

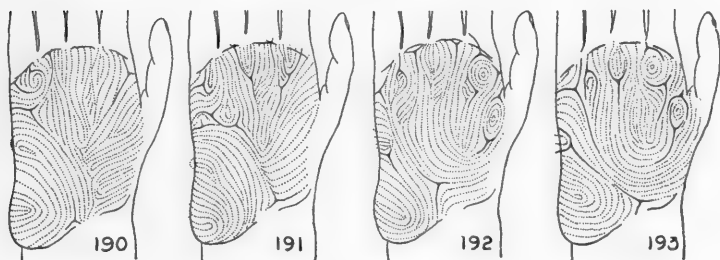
I: V (1); W (3); S (1).

II: O (1); V (1);  $L^d$  (1); W (3).

III: O (2); V (1);  $L^d$  (2); W (1).

IV:  $L^d$  (1);  $L^p$  (2); W (2); S (1).

CA (4):  $2^p$ : V (1).  $2^p$ ,  $3^p$ , and  $4^p$ : V, V, and V (2); V, V, and  $L^d$  (1). P-th:  $L^d$  (4).



Figs. 190-193 Lagothrix, manus.

## Pes (5)

## Figures 194-197

The plantar surface shows a flattening comparable to the condition described in *Ateles*.

H<sup>d</sup>: O (1); V (1); L<sup>f</sup> (2); W (1).

H<sup>p</sup>: O (4); L<sup>f</sup> (1).

C: O (4); No ridge formation (1).

Th: O (3); L<sup>p</sup> (1); W (1). All these represent Th<sup>p</sup> alone; in the case having a whorl, Th<sup>d</sup> also is patterned, L<sup>d</sup>.

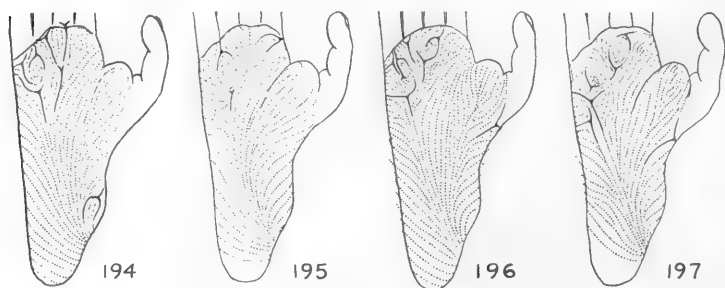
I: V (2); L<sup>p</sup> (2); L<sup>d</sup>W (1).

II: O (2); V (2); L<sup>p</sup> (1).

III: O (1); V (1); W (1); S (2).

IV: W (2); S (3).

CA: O (5).



Figs. 194-197 *Lagothrix*, pes.

## CEBUS

## Manus

## Figures 198-212

The border pads are as described in *Saimiri*. The distal central area is slightly more elevated than the proximal region, pads 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup> being faintly suggested.

(H, 39) H<sup>d</sup> + H<sup>p</sup>: L<sup>u</sup> (6); W (12); S (13).

H<sup>d</sup>: O (6); L<sup>u</sup> (1); L<sup>p</sup> (1).

H<sup>p</sup>: L<sup>u</sup> (2); W (4); S (2).

(Th, 37) Th + I: W (1).

Th: O (35); L<sup>d</sup> (1).

(I, 37) I + Th: See above.

I: W (33); S (3).

II (39): W (39).

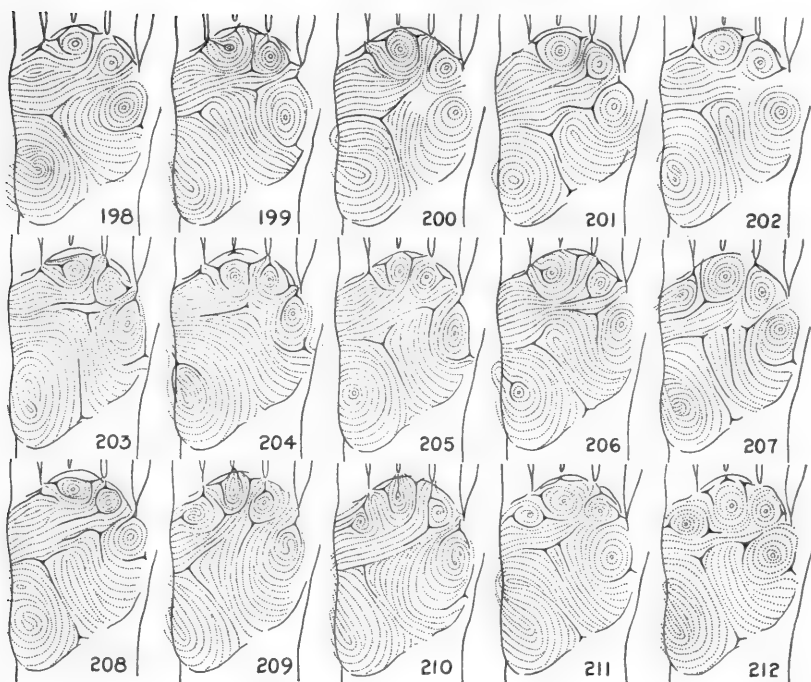
III (38): W (38).

IV (38): O (7); V (11); L<sup>r</sup> (1); L<sup>u</sup> (5); W (14).

CA (34): O (13). 2<sup>p</sup>: V (1). 3<sup>p</sup>: V (1); L<sup>p</sup> (3).

4<sup>p</sup>: V (2). 2<sup>p</sup> and 3<sup>p</sup>: V (1). 3<sup>p</sup> and 4<sup>p</sup>:

V (2). P-th: L<sup>p</sup> (9); L<sup>p</sup>L<sup>p</sup> (2).



Figs. 198-212 Cebus, manus.

## Pes

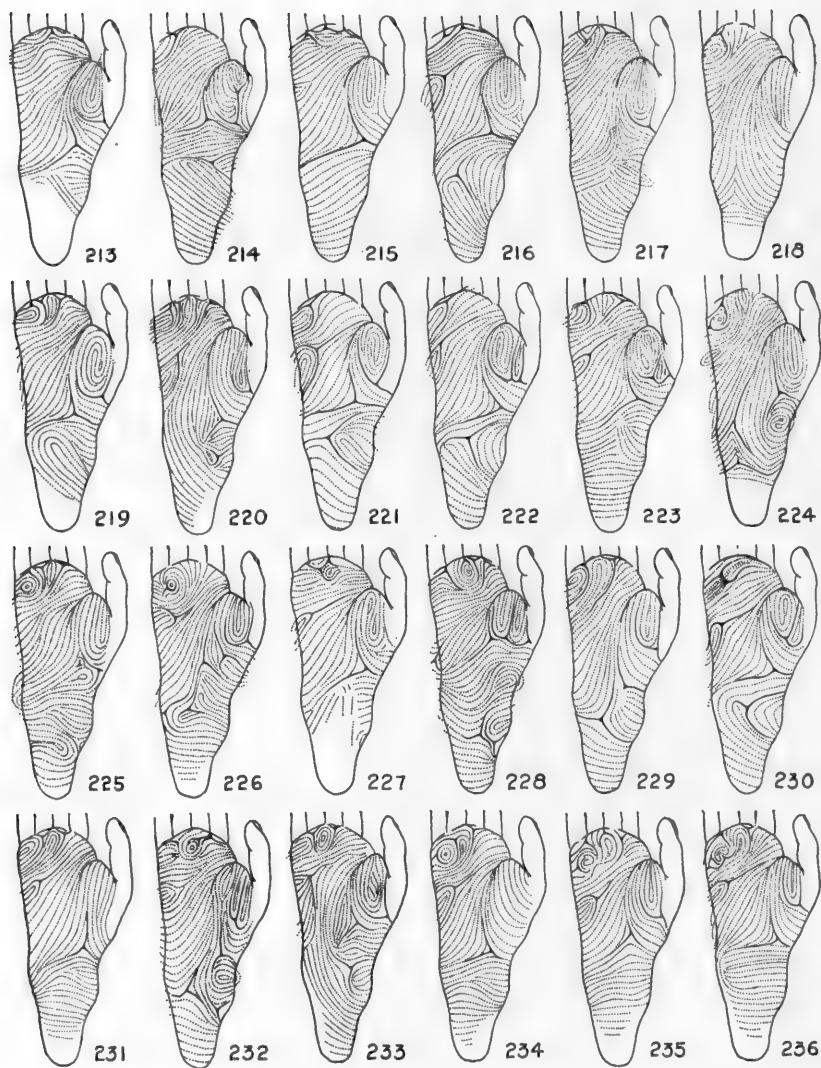
### Figures 213-236

(H, 36) H<sup>d</sup> + H<sup>p</sup>: L<sup>f</sup> (1); L<sup>t</sup> (1).

H<sup>d</sup>: O (13); V (4); L<sup>f</sup> (8); L<sup>p</sup> (6); L<sup>t</sup> (1);  
W (1); S (1).

H<sup>p</sup>: O (25); V (2); L<sup>p</sup> (1); L<sup>t</sup> (6).

C (35): O (26); L<sup>f</sup> (3); L<sup>t</sup> (5); S (1).

Figs. 213-236 *Cebus*, pes.



- (Th, 38) Th<sup>p</sup> + Th<sup>d</sup>: L<sup>f</sup> (1); L<sup>t</sup> (1); VL<sup>t</sup> (1); W (2).  
 Th<sup>p</sup>: O (15); V (7); L<sup>f</sup> (2); L<sup>t</sup> (6); S (3).  
 Th<sup>d</sup>: O (23); T (1); L<sup>d</sup> (1); L<sup>f</sup> (2); L<sup>t</sup> (2);  
 W (1); S (1); L<sup>f</sup>T (1); ? (1).

In occasional examples parts of the thenar pattern (particularly Th<sup>p</sup>) are displaced fibularward toward the parathenar or even the hypothenar areas (figs. 221 and 236). See CA, below.

- I (37): O (6); L<sup>d</sup> (15); W (3); S and various duplex patterns (13).  
 II (36): O (33); V (1); L<sup>fp</sup> (2).  
 III (36): O (15); V (6); L<sup>d</sup> (2); L<sup>p</sup> (6);  
 L<sup>t</sup> (2); W (5).  
 IV (36): O (2); V (8); L<sup>d</sup> (1); L<sup>f</sup> (18);  
 W (5); S (1); TS (1).  
 CA (36): O (20). 4<sup>p</sup>: V (1); L<sup>t</sup> (1). P-th:  
 V (8); L<sup>t</sup> (5); L<sup>f</sup>L<sup>t</sup> (1).

SIMIAE (ANTHROPOIDEA; SIMIANS)

CATARRHINAE

LASIOPYGIDAE (OLD WORLD MONKEYS;  
CATARRHINE MONKEYS)

LASIOPYGINAE

PAPIO (BABOON)

THEROPITHECUS (GELADA)

CYNOPITHECUS (BLACK APE)

MAGUS (CELEBES MACAQUE)

PITHECUS (MACAQUE)

CERCOCEBUS (MANGABEY)

LASIOPYGA (GUENON)

ERYTHROCEBUS (RED GUENON)

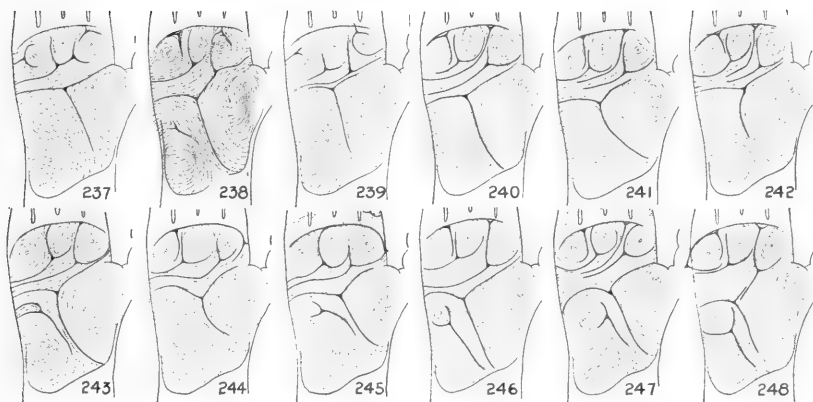
## PAPIO

## Manus

## Figures 237-248

The prominence of the pads of the border series is noteworthy. Each of the typical pads, including the divisions  $H^d$  and  $H^p$ , is clearly circumscribed, though Th and I are merged into a single large pad.

- (H, 23)  $H^d$ : O (2);  $L^p$  (1);  $L^r$  (7);  $L^u$  (3); W (10).  
 $H^p$ :  $L^u$  (14); S (9).  
 (Th, 28) Th + I: S (4).  
 Th: O (24).  
 (I, 28) I + Th: See above.  
 I: W (13); S (11).  
 II (30): W (30).  
 III (28):  $L^d$  (2); W (24); S (2).  
 IV (30): W (30).  
 CA (28): O (28).



Figs. 237-248 Papio, manus.

## Pes

## Figures 249-260

The typical border pads are pronounced. Pads Th and H are blended across the midline, forming a massive prominence.

(H, 26)  $H^d + H^p$ : T (1);  $L^t$  (4); S (5);  $L^f W$  (1);  $SL^t$  (1).  
 $H^d$ : O (2);  $L^t$  (2); W (1); S (3);  $L^t L^t$  (2);  
 $WL^t$  (1);  $L^f W$  (2);  $SL^f$  (1).

$H^p$ : O (14).

C (24): O (24).

Th (26): O (5); V (7);  $L^t$  (12); W (1); S (1).

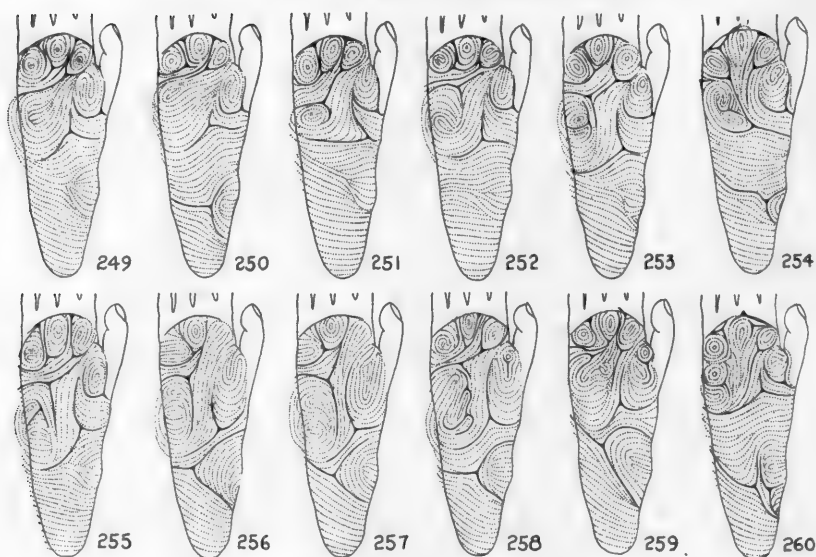
I (28):  $L^d$  (6); W (11); S (10);  $WL^d$  (1).

II (24):  $L^f$  (2);  $L^p$  (4); W (13); S (5).

III (28):  $L^p$  (1); W (25); S (2).

IV (27):  $L^f$  (4);  $L^t$  (2); W (17); S (4).

CA (27): In only one case (Mutrux-Bornoz, pl. 16) is there a feature of note in CA, an  $L^d$  with its head in the P-th region. It is possible that in several soles pattern features which have been assigned to H actually are members of the CA series (figs. 254, 258, 259).



Figs. 249-260 Papio, pes.

#### THEROPITHECUS

Manus (1) — Bychowska, figure 21

$H^d$ :  $L^u$ .

$H^p$ :  $L^u$ .

Th + I: S.

II: W.  
 III: L<sup>d</sup>  
 IV: W.  
 CA: O.

## CYNOPITHECUS

Manus (2) — Kidd, figure 30; Hepburn, plate 48

H<sup>d</sup>: O (2).  
 H<sup>p</sup>: W (1); S (1).  
 Th + I: W (2).  
 II: W (2).  
 III: W (2).  
 IV: W (2).  
 CA: O (2).

## Pes (3)

Hepburn, plate 47; Kidd, figure 31; Schlaginhaufen, figure 126

H<sup>d</sup> + H<sup>p</sup>: L<sup>t</sup> (1).  
 H<sup>d</sup>: W (1); S (1).  
 H<sup>p</sup>: O (1); L<sup>p</sup> (1).  
 C: O (3).  
 Th: L<sup>d</sup> (1); L<sup>t</sup> (2).  
 I: L<sup>d</sup> (1); W (1); S (1).  
 II: L<sup>fp</sup> (3).  
 III: W (2); S (1).  
 IV: W (1); S (2).  
 CA: O (3).

## MAGUS

## Manus (2)

Figures 261-262

H<sup>d</sup>: O (2).  
 H<sup>p</sup>: L<sup>n</sup> (1); S (1).  
 Th: O (1); V (1).  
 I: W (2).  
 II: W (2).  
 III: W (2).  
 IV: W (2).  
 CA: O (2).

## Pes (2)

## Figures 263-264

H<sup>d</sup> + H<sup>p</sup>: S (1).H<sup>d</sup>: L<sup>p</sup> (1).H<sup>p</sup>: O (1).

C: O (2).

Th: L<sup>t</sup> (2).

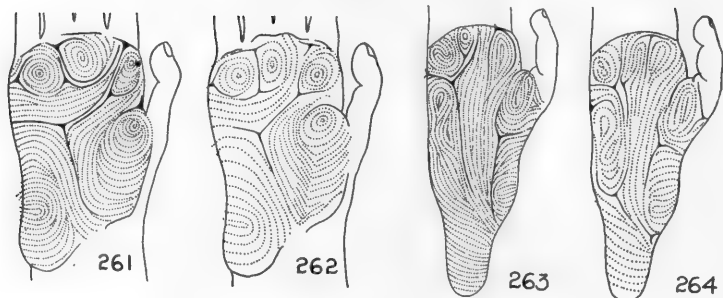
I: S (2).

II: L<sup>p</sup> (2).

III: W (1); S (1).

IV: W (1); S (1).

CA: O (2).

Figs. 261-262 *Magus maurus*, manus.

Figs. 263-264 Same, pes.

## PITHECUS (MACACA)

## Manus

## Figures 265-325

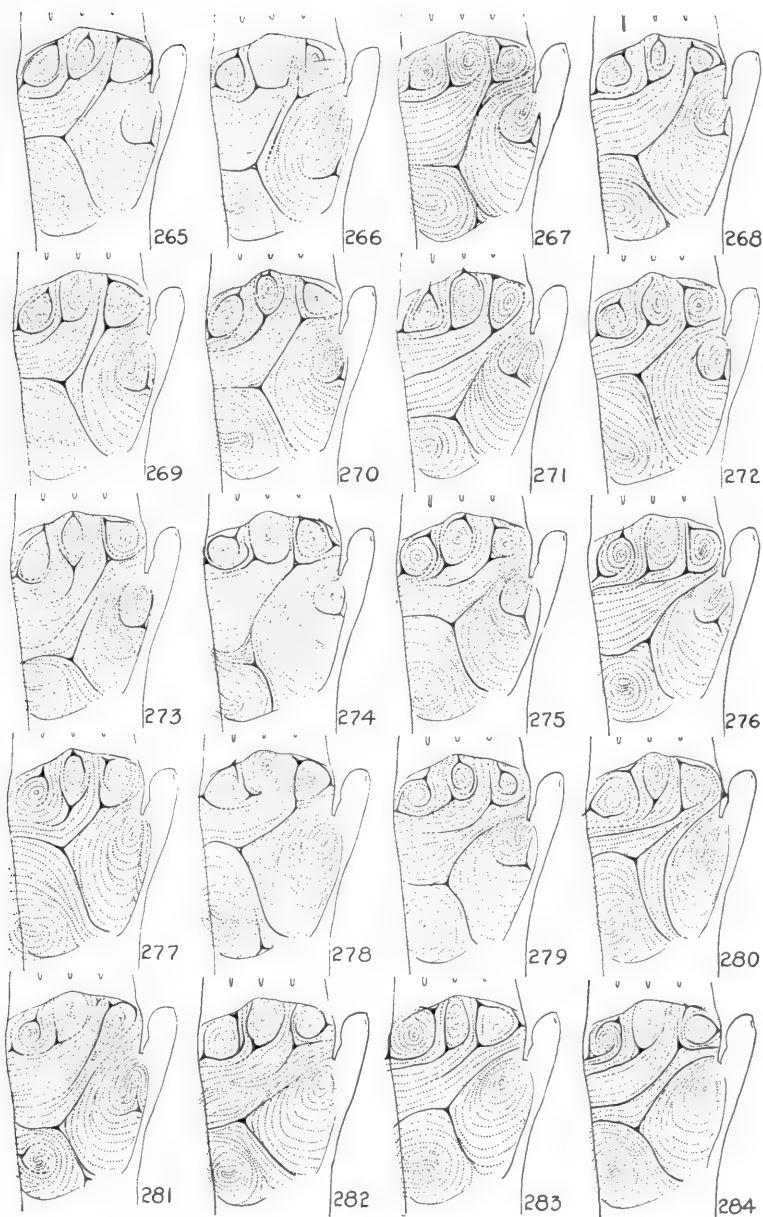
As will be noted in figure 325, the details (minutiae) of individual ridges correspond in their variations to those which are more familiar in the human epidermis; this statement would apply equally to the epidermal ridges of all primates.

(H, 86) H<sup>d</sup>: O (30); V (12); T (3); L<sup>p</sup> (2); L<sup>r</sup> (20);  
L<sup>u</sup> (4); W (7); S (8).

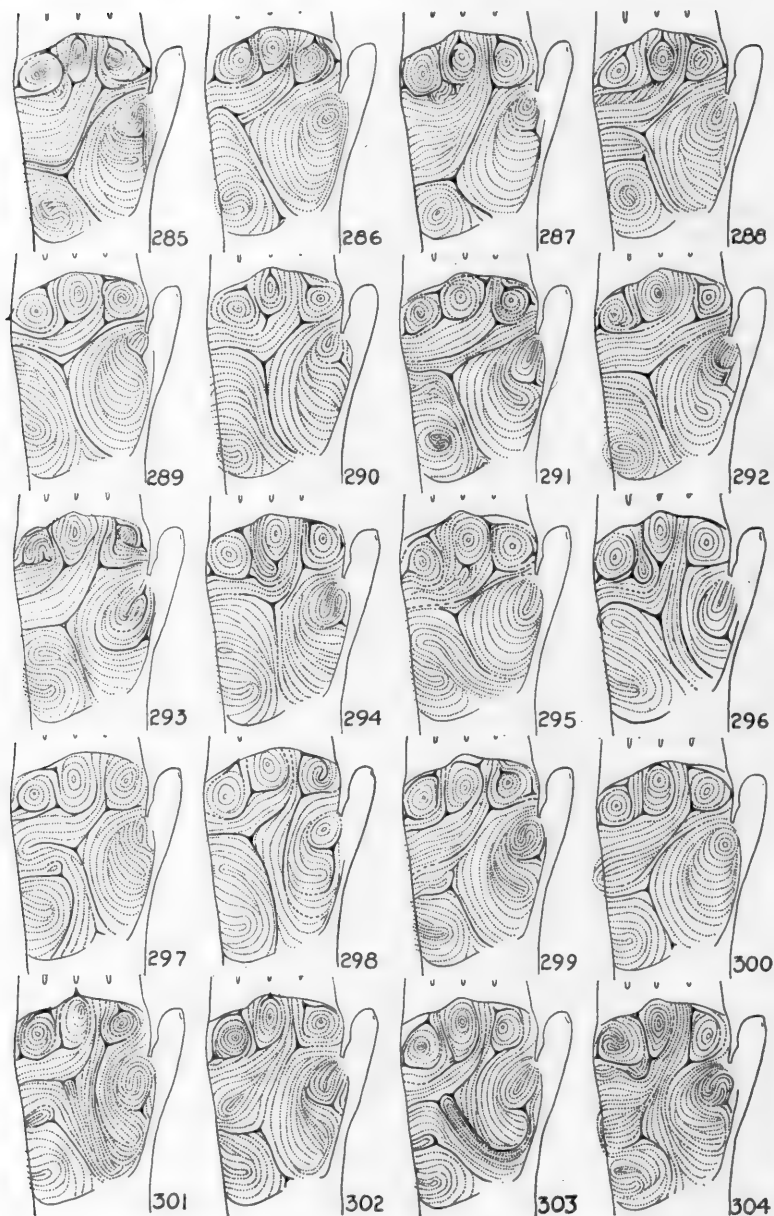
H<sup>p</sup>: L<sup>u</sup> (32); W (18); L<sup>u</sup>L<sup>u</sup> (1); S (35).

(Th, 88) Th + I: L<sup>d</sup> (2); L<sup>r</sup> (1); S (1).

Th: O (48); L<sup>d</sup> (35); W (1).

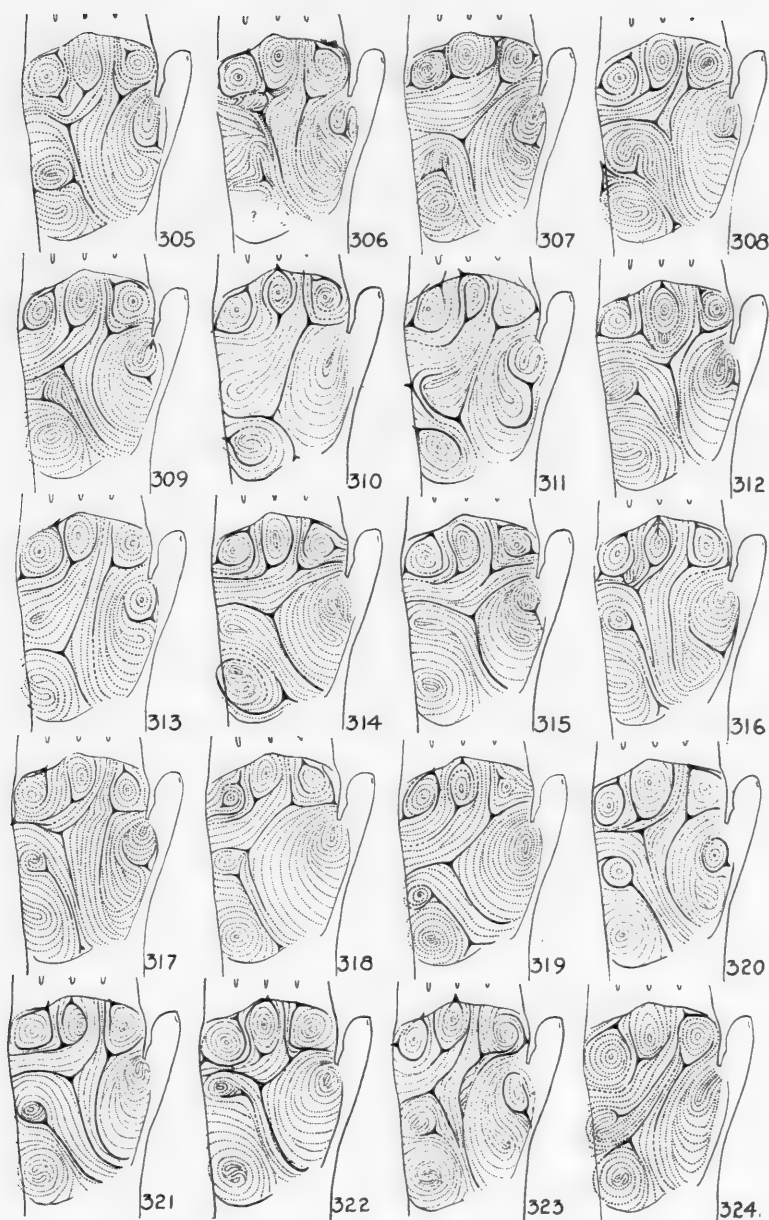


Figs. 265-284 *Pithecus (Macaca)*, manus.



Figs. 285-304 *Pithecus* (*Macaca*), manus.



Figs. 305-324 *Pithecus (Macaca)*, manus.

(I, 88) I + Th: See above.

I: V (2); L<sup>d</sup> (38); L<sup>p</sup> (1); L<sup>r</sup> (1); W (25);  
S (21).

II (89): L<sup>p</sup> (1); L<sup>r</sup> (3); L<sup>a</sup> (1); W (76); S (8).

III (91): L<sup>d</sup> (4); W (86); S (1).

IV (90): W (85); S (5).

CA (91): O (70). 2<sup>p</sup>: V (1); L<sup>r</sup> (1). 3<sup>p</sup>:  
V (3); L<sup>d</sup> (1). 4<sup>p</sup>: V (9); L<sup>p</sup> (2).  
3<sup>p</sup> + 4<sup>p</sup>: V (2). Between 3<sup>p</sup> and 4<sup>p</sup>:  
L<sup>d</sup> (2). The identification of some  
of these vestiges and patterns as  
elements of the distal part of the  
central area is uncertain, owing to  
their frequent placement (e.g., figs.  
287, 294, 296, 316) in situations out  
of alignment with 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>.



Fig. 325 *Pithecius rhesus* (*Macaca mulatta*), print of left manus.

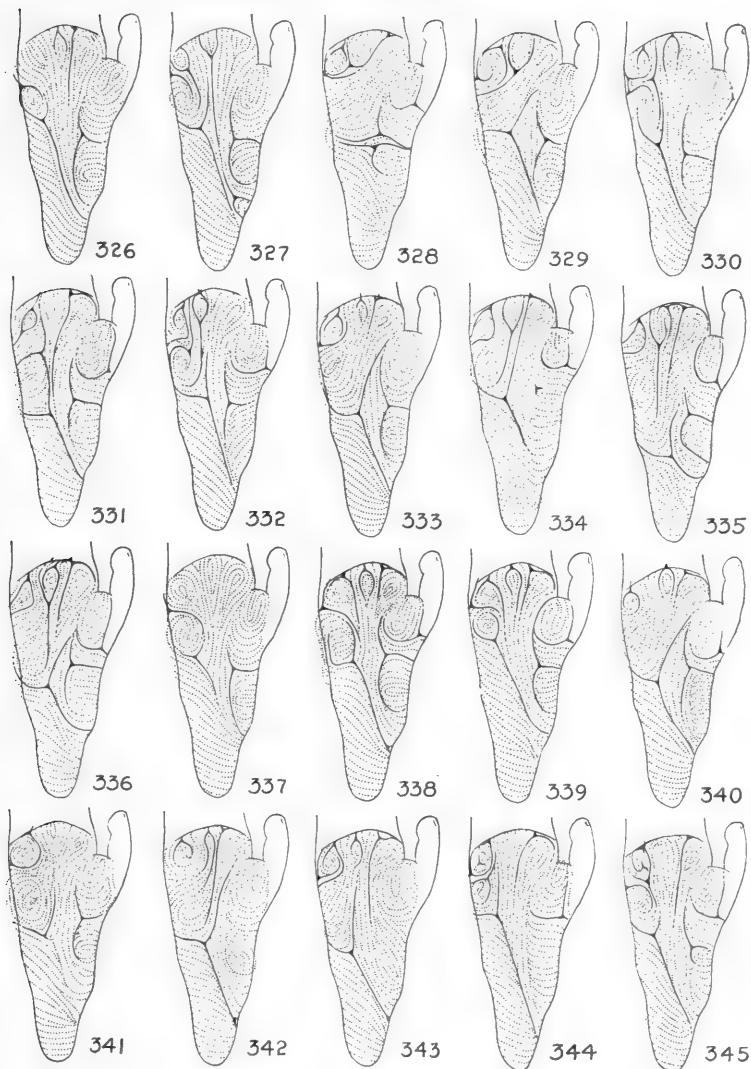
## Pes

## Figures 326-385

(H, 90)  $H^d + H^p$ :  $L^f$  (1);  $L^t$  (1);  $W$  (1).

$H^d$ :  $O$  (5);  $V$  (1);  $L^d$  (27);  $L^f$  (1);  $L^t$  (13);  
 $W$  (6);  $S$  (34).

$H^p$ :  $O$  (76);  $V$  (2);  $T$  (1);  $L^d$  (1);  $L^p$  (1);  
 $L^t$  (5);  $W$  (1).



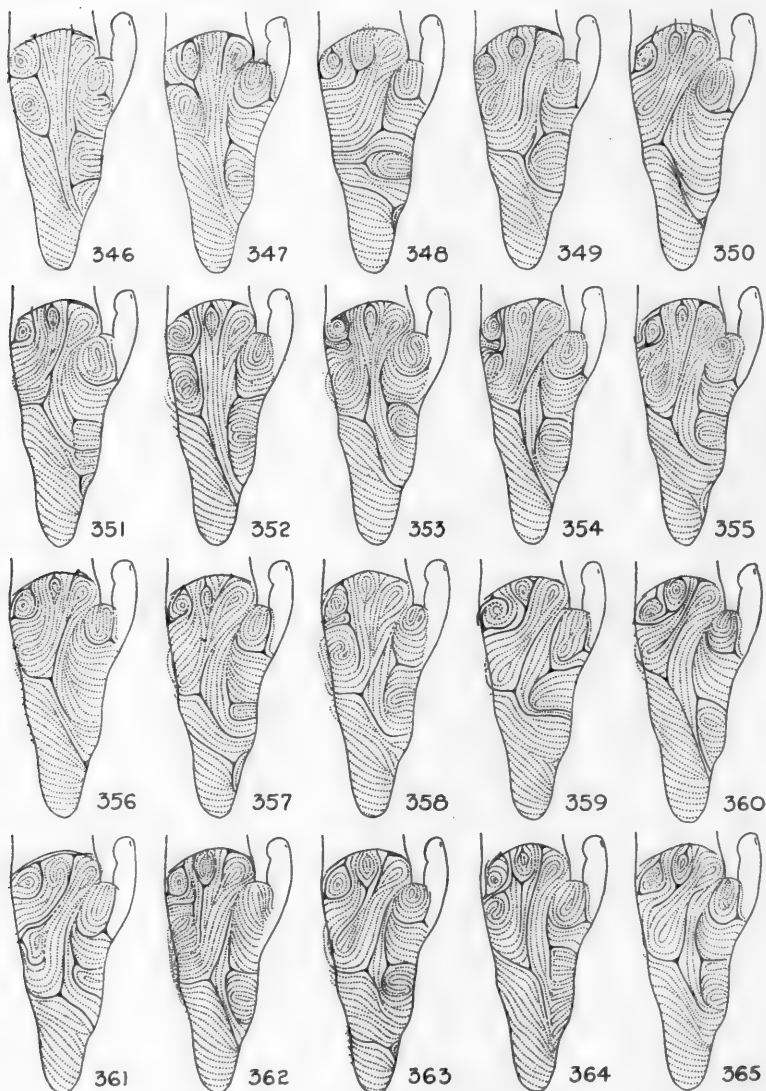
Figs. 326-345 *Pithecus* (*Macaca*), pes.

C (89): O (73); V (1); L<sup>f</sup> (14); L<sup>t</sup> (1).

Th (90): O (11); V (5); L<sup>d</sup> (1); L<sup>t</sup> (59); W (9); S (5).

I (89): O (1); L<sup>d</sup> (39); L<sup>t</sup> (1); W (13); S (33);  
L<sup>p</sup>W (1); L<sup>d</sup>S (1).

II (91): L<sup>d</sup> (1); L<sup>f</sup> (50); L<sup>p</sup> (35); W (4); S (1).

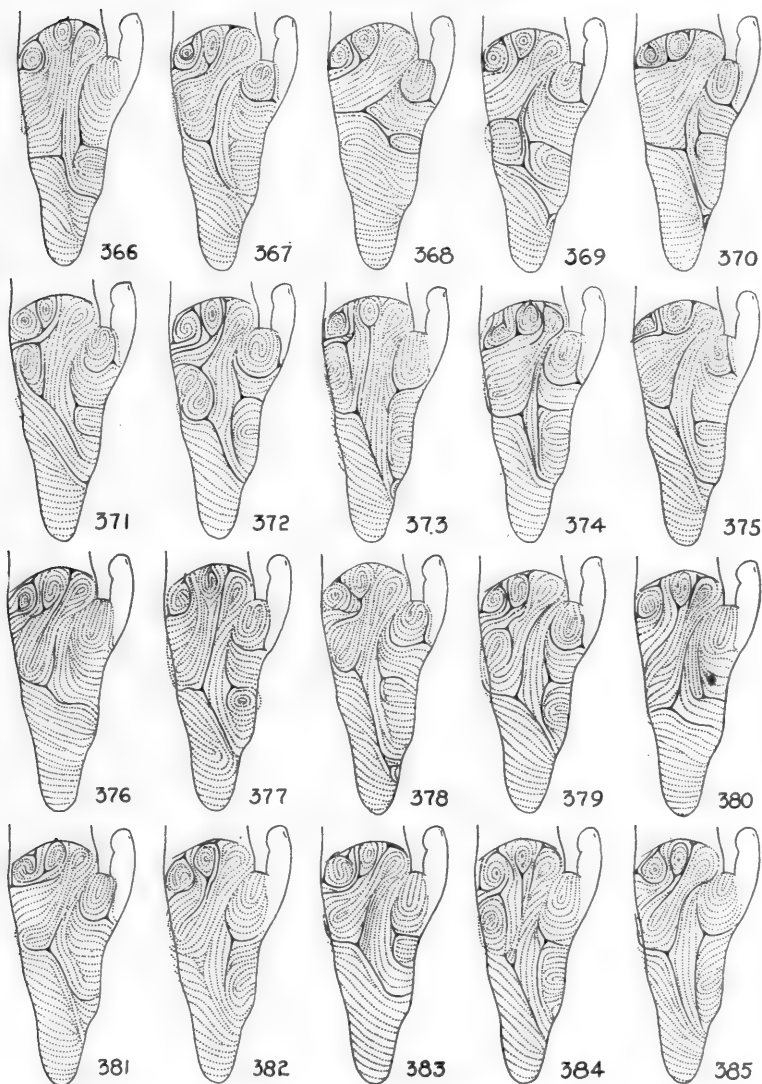


Figs. 346-365 Pithecius (Macaca), pes.

III (93): O (2); V (12); L<sup>d</sup> (12); L<sup>f</sup> (2); L<sup>p</sup> (13);  
W (44); S (6); L<sup>p</sup>W (1); L<sup>p</sup>S (1).

IV (92): V (1); L<sup>f</sup> (9); L<sup>p</sup> (3); L<sup>t</sup> (2); W (54);  
S (15); TL<sup>d</sup> (1); TL<sup>t</sup> (1); WV (1);  
WL<sup>d</sup> (1); WL<sup>f</sup> (4).

CA (91): O (66). P-th: V (16); L<sup>d</sup> (7); L<sup>p</sup> (1); L<sup>t</sup> (1).



Figs. 366-385 Pithecius (Macaca), pes.

## CERCOCEBUS

## Manus (4)

## Figures 386-387

H<sup>d</sup>: O (2); W (2).H<sup>p</sup>: L<sup>a</sup> (1); W (1); S (2).Th + I: L<sup>d</sup> (1); S (1).

Th: O (2).

I + Th: See above.

I: L<sup>d</sup> (1); W (1).

II: W (4).

III: W (4).

IV: L<sup>a</sup> (4).

CA: O (4).

## Pes (5)

## Figures 388-389

H<sup>d</sup> + H<sup>p</sup>: L<sup>d</sup> (1).H<sup>d</sup>: L<sup>d</sup> (1); W (3).H<sup>p</sup>: L<sup>p</sup> (1); L<sup>t</sup> (2); L<sup>t</sup>L<sup>p</sup> (1).C: O (3); V (1); L<sup>d</sup>L<sup>d</sup> (1).Th: V (1); L<sup>t</sup> (3); S (1).I: L<sup>d</sup> (4); S (1).II: L<sup>p</sup> (5).III: L<sup>d</sup> (1); W (4).IV: L<sup>t</sup> (5).

CA: O (5).

Figs. 386-387 *Cercopithecus aethiops*, manus.

Figs. 388-389 Same, pes.

## LASIOPYGA

## Manus (17)

## Figures 390-404

$H^d + H^p$ : W (1); S (3).

$H^d$ : O (13).

$H^p$ :  $L^u$  (8); W (4); S (1).

Th: O (11);  $L^d$  (6).

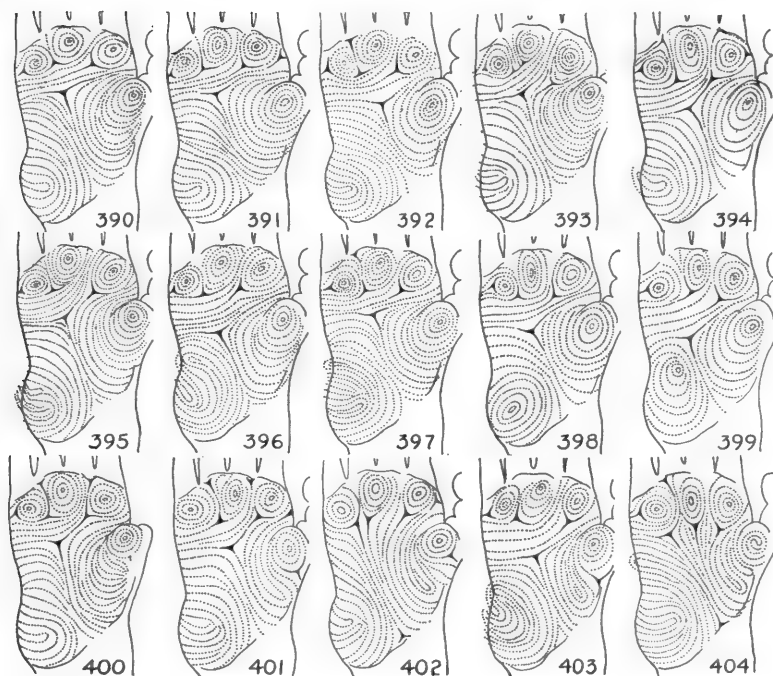
I: W (15); S (1).

II: W (16); S (1).

III: W (17).

IV: W (17).

CA: O (17).

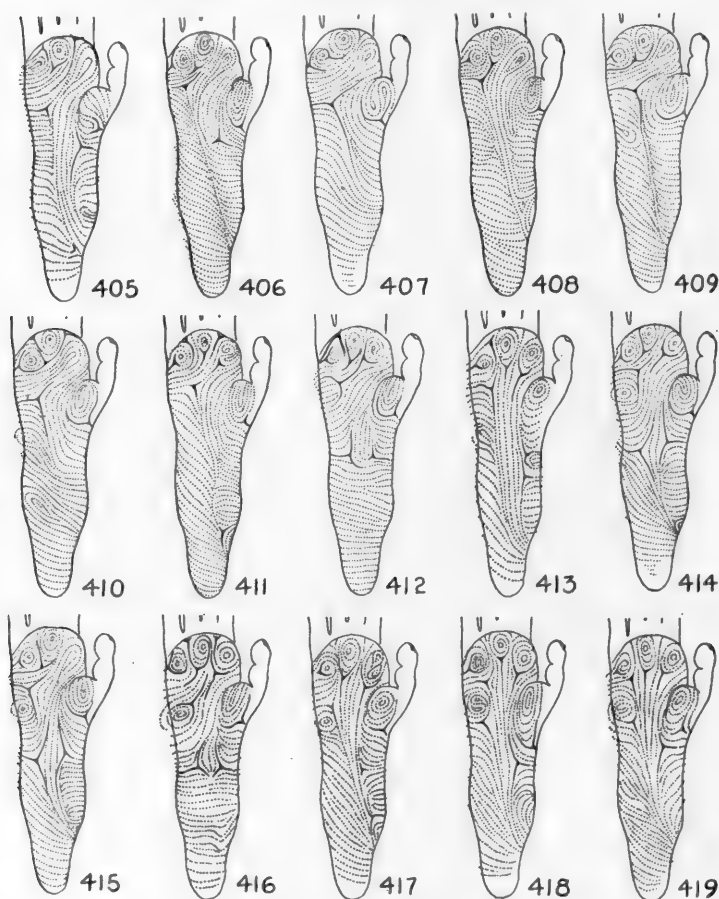


Figs. 390-404 Lasiopyga, manus.

## Pes

## Figures 405-419

- (H, 19)  $H^d + H^p$ :  $L^f$  (1);  $L^t$  (3); S (1).  
 $H^d$ : O (5);  $L^f$  (1);  $L^t$  (1); W (5); S (2).  
 $H^p$ : O (14).  
C (18): O (17);  $L^t$  (1).  
Th (19): O (5); V (3);  $L^f$  (1);  $L^t$  (9); W (1).  
I (19):  $L^d$  (8); W (7); S (4).  
II (19):  $L^{fp}$  (11); W (5); S (3).  
III (19): W (19).  
IV (19):  $L^f$  (3); W (16).  
CA (19): O (15). P-th:  $L^d$  (4).

Figs. 405-419 *Lasiopyga*, pes.



## ERYTHROCEBUS

## Manus (6)

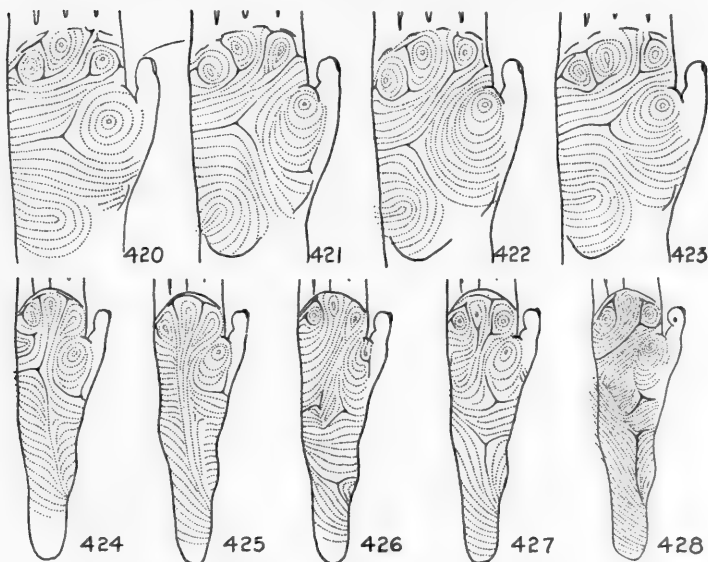
## Figures 420-423

H <sup>d</sup> : O (6).	II: W (6).
H <sup>p</sup> : L <sup>a</sup> (6).	III: W (6).
Th: O (6).	IV: W (6).
I: W (6).	CA: O (6).

## Pes (6)

## Figures 424-428

H <sup>d</sup> : O (1); L <sup>d</sup> (1); L <sup>r</sup> (3); L <sup>t</sup> (1).
H <sup>p</sup> : O (5); V (1).
C: O (6).
Th: O (5); L <sup>t</sup> (1).
I: W (5); L <sup>d</sup> L <sup>d</sup> (1).
II: L <sup>p</sup> (4); W (2).
III: L <sup>p</sup> (2); W (3); S (1).
IV: W (6).
CA: P-th: O (3); V (1); L <sup>d</sup> (2).



Figs. 420-423 Erythrocebus patas, manus.  
 Figs. 424-428 Same, pes.

SIMIAE (ANTHIROPOIDEA; SIMIANS)

CATARRHINAE

LASIOPYGIDAE

COLOBINAE

PYGATHRIX (LANGUR)

NASALIS (PROBOSCIS MONKEY)

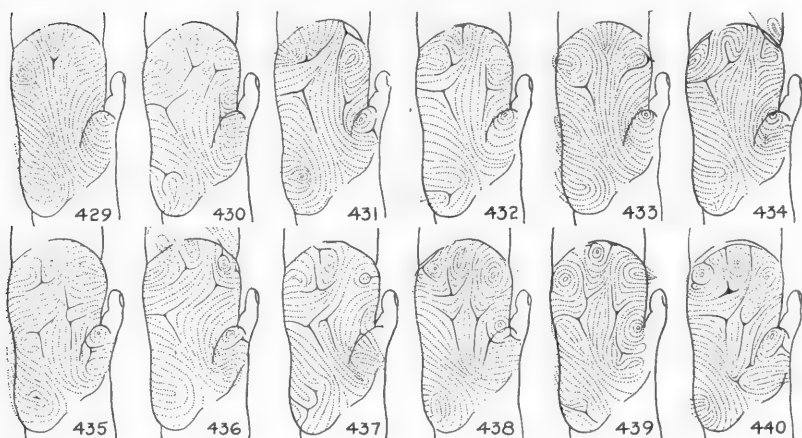
COLOBUS (GUEREZA)

## PYGATHRIX

## Manus

## Figures 429-440

- (H, 15)  $H^d$ : O (8); V (1); T (1);  $L^p$  (1);  $L^r$  (2);  $L^u$  (2).  
 $H^p$ : T (1);  $L^p$  (2);  $L^u$  (7); W (3); S (2).  
 (Th, 15) Th + I: O (1).  
 Th: O (4);  $L^r$  (1); W (8); S (1).  
 (I, 15) I + Th: See above.  
 I:  $L^d$  (1);  $L^r$  (1); W (11); S (1).  
 II (15): V (1);  $L^d$  (1);  $L^r$  (2);  $L^u$  (2); W (6); S (2);  
 $L^rW$  (1).  
 III (15):  $L^d$  (8);  $L^u$  (1); W (5); S (1).  
 IV (15):  $L^r$  (1);  $L^u$  (9); W (3); S (1);  $WL^r$  (1).  
 CA (14): O (10).  $2^p$ :  $L^r$  (1).  $3^p$ : V (1).  
 P-th:  $L^d$  (1);  $L^p$  (1).



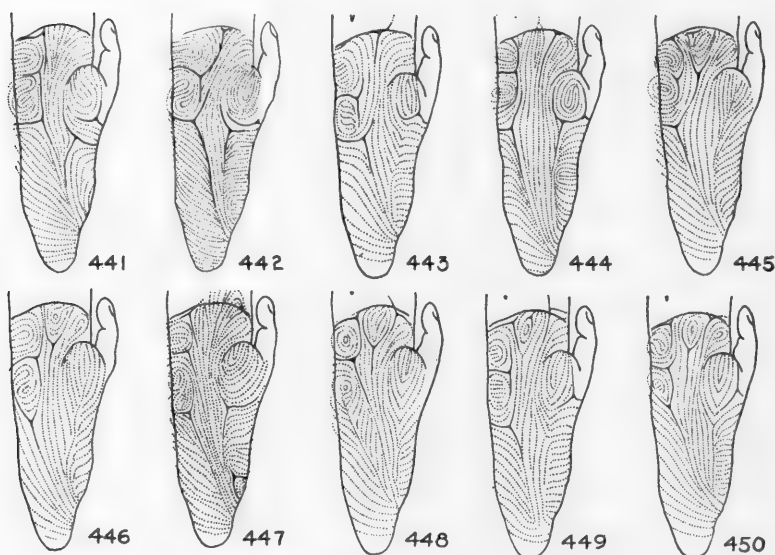
Figs. 429-440 Pygathrix, manus.

## Pes (14)

## Figures 441-450

- $H^d + H^p$ : S (2).  
 $H^d$ :  $L^{pt}$  (2); W (6); S (4).  
 $H^p$ : O (12).  
 C: O (13);  $L^d$  (1).  
 Th: O (2); V (6);  $L^t$  (4);  $VL^t$  (1);  $L^tV$  (1).

- I: V (1); L<sup>d</sup> (6); W (2); S (2); VL<sup>d</sup> (3).  
 II: O (4); L<sup>t</sup> (4); L<sup>p</sup> (6).  
 III: O (8); L<sup>d</sup> (2); W (4).  
 IV: V (1); L<sup>t</sup> (7); W (5); S (1).  
 CA: O (14).



Figs. 441-450 *Pygathrix*, pes.

#### NASALIS

#### Manus (2)

#### Figures 451-452

- H<sup>d</sup>: O (2).  
 H<sup>p</sup>: L<sup>u</sup> (2).  
 Th: V (1); T (1).  
 I: L<sup>d</sup> (1); W (1).  
 II: L<sup>p</sup> (2).  
 III: L<sup>p</sup> (2).  
 IV: L<sup>p</sup> (1); S (1).  
 IV<sup>u</sup>: In one hand (fig. 452) the L<sup>r</sup> pattern lying in this position may be tentatively assigned to IV<sup>u</sup>, though the possibility of its identity as an H<sup>d</sup> can not be excluded.  
 CA: No ridges formed.

## Pes (2)

## Figures 453-454

 $H^d + H^p$ :  $L^t$  (1). $H^d$ :  $L^t$  (1). $H^p$ :  $L^p$  (1).

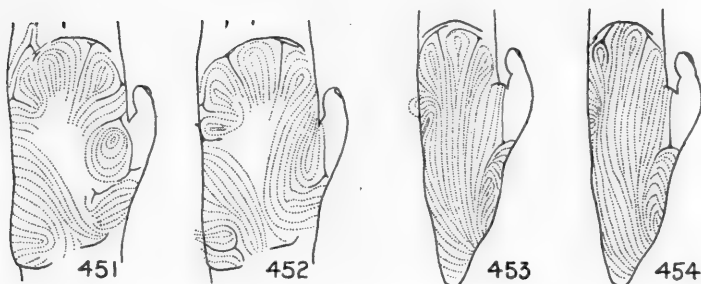
C: O (2).

Th: V (1);  $L^p$  (1).

I: O (2).

II:  $L^p$  (2).III:  $L^p$  (2).IV:  $L^p$  (1); W (1).

CA: O (2).

Figs. 451-452 *Nasalis larvatus*, manus.

Figs. 453-454 Same, pes.

## COLOBUS

## Manus (5)

## Figures 455-457

 $H^d + H^p$ : S (1). $H^d$ : O (3);  $L^t$  (1). $H^p$ :  $L^u$  (3); S (1).Th: O (3);  $L^t$  (1); S (1).I:  $L^d$  (1); W (4).II:  $L^t$  (2); W (1); S (2).III:  $L^d$  (5).IV:  $L^u$  (5).CA: O (4).  $3^p$ :  $L^p$  (1).

## Pes (3)

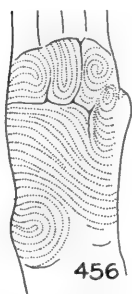
## Figure 458

H<sup>d</sup>: O (2); L<sup>t</sup> (1).H<sup>p</sup>: O (3).

C: O (3).

Th: O (1); V (1); VL<sup>t</sup> (1).I: O (1); L<sup>d</sup> (1); W (1).II: O (1); L<sup>p</sup> (2).III: O (1); L<sup>d</sup> (2).IV: L<sup>t</sup> (2); L<sup>p</sup> (1).

CA: O (3).



Figs. 455-457 Colobus, manus.

Fig. 458 Same, pes.

SIMIAE (ANTHROPOIDEA ; SIMIANS)

CATARRHINAE

HYLOBATIDAE

HYLOBATES (GIBBON)

SYMPHALANGUS (SIAMANG)

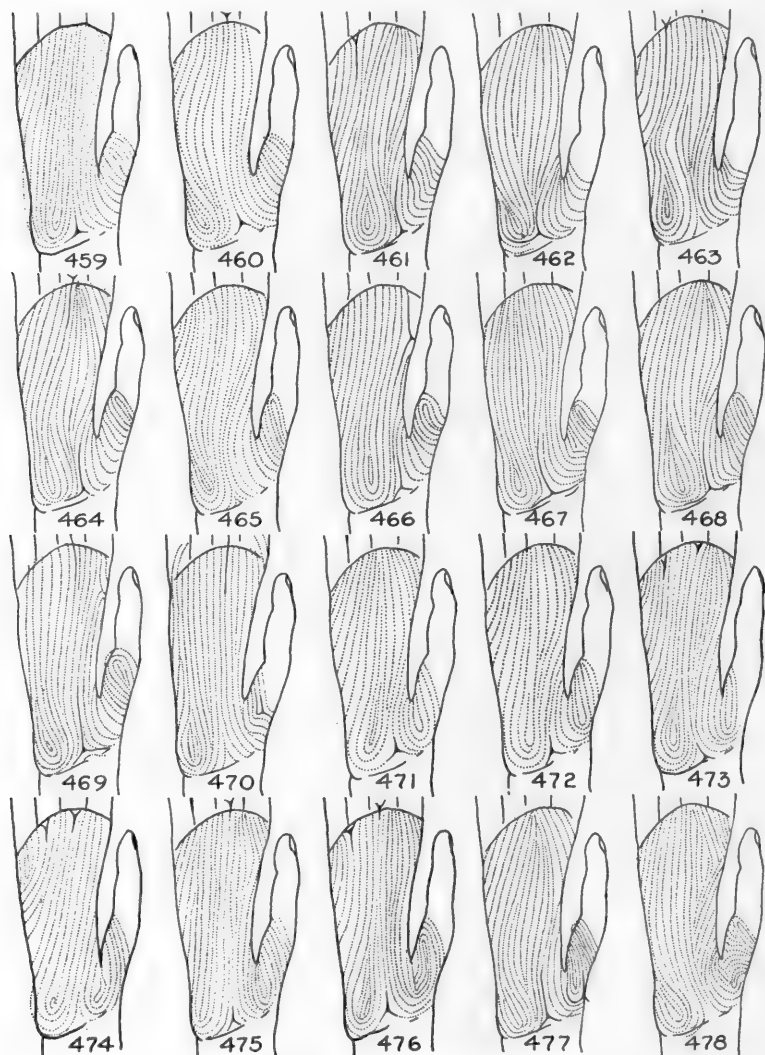
(The term "higher primates" has been used to embrace Hylobatidae, Pongidae and Homo.)

## HYLOBATES

## Manus (44)

## Figures 459-498

The palmar surface is generally flattened, the most evident indication of a pad being H<sup>p</sup>. Elongation of the palm and



Figs. 459-478 Hylobates, manus.



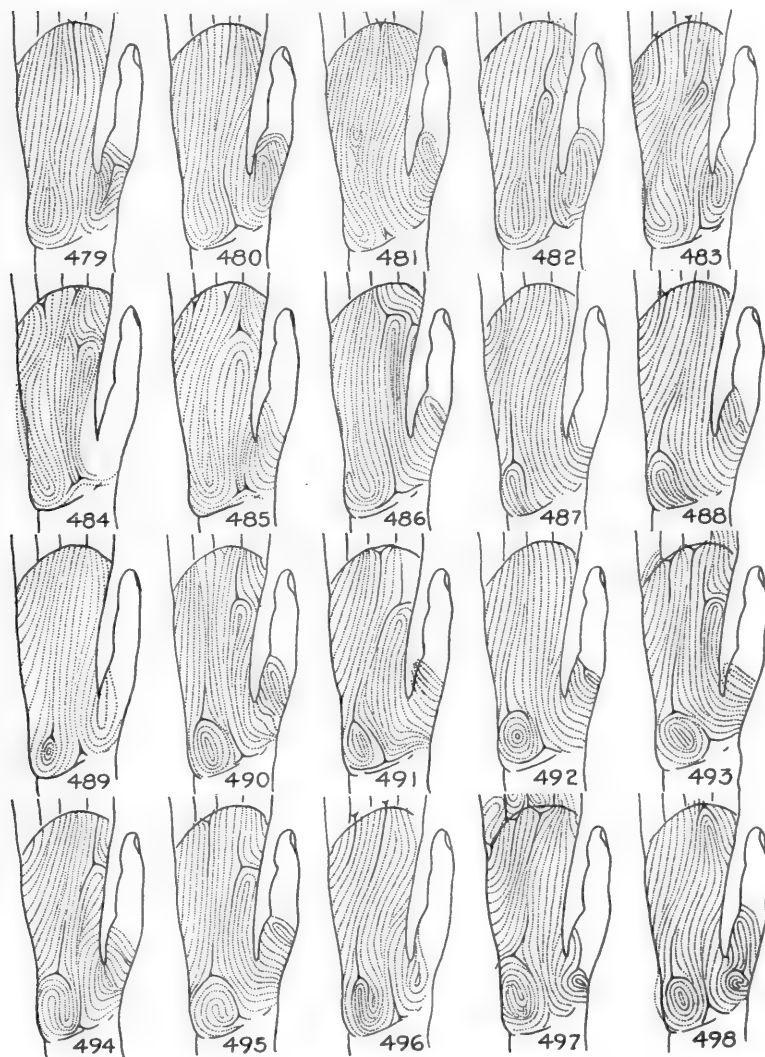
extension into the metacarpal level of the first interdigital interval are characteristic of the Hylobatidae.

H<sup>d</sup>: O (44).

H<sup>p</sup>: L<sup>d</sup> (28); L<sup>p</sup> (2); W (10); S (4).

Th + I: O (13); T (1); W (1); S (1).

Th: O (18); V (1); L<sup>d</sup> (7); W (2).



Figs. 479-498 *Hylobates*, manus.

I + Th: See above.

I: O (6); V (5); L<sup>d</sup> (2); L<sup>p</sup> (2); L<sup>r</sup> (13).

II: O (43); L<sup>p</sup> (1).

III: O (44).

IV: O (42); V (2).

CA: O (30). 2<sup>p</sup>: V (3); L<sup>p</sup> (10). In one hand (fig. 481) a series of three incompletely formed loops lies in the axis of 4<sup>p</sup>, but too far proximally to justify identification as 4<sup>p</sup>; their identity remains obscure because they are placed farther ulnarward than the typical parathenar territory.

### Pes

#### Figures 499-533

The whole plantar surface is generally flattened, lacking distinct pads.

(H, 45) H<sup>d</sup> + H<sup>p</sup>: L<sup>d</sup> (1).

H<sup>d</sup>: O (41); V (1); L<sup>d</sup> (1); L<sup>t</sup> (1).

H<sup>p</sup>: O (36); V (2); L<sup>d</sup> (2); L<sup>tp</sup> (4).

C (45): O (36); L<sup>at</sup> (8); L<sup>d</sup>V (1).

Th (45): O (13); V (1); L<sup>d</sup> (1); L<sup>p</sup> (16);  
L<sup>t</sup> (8); W (3); S (3).

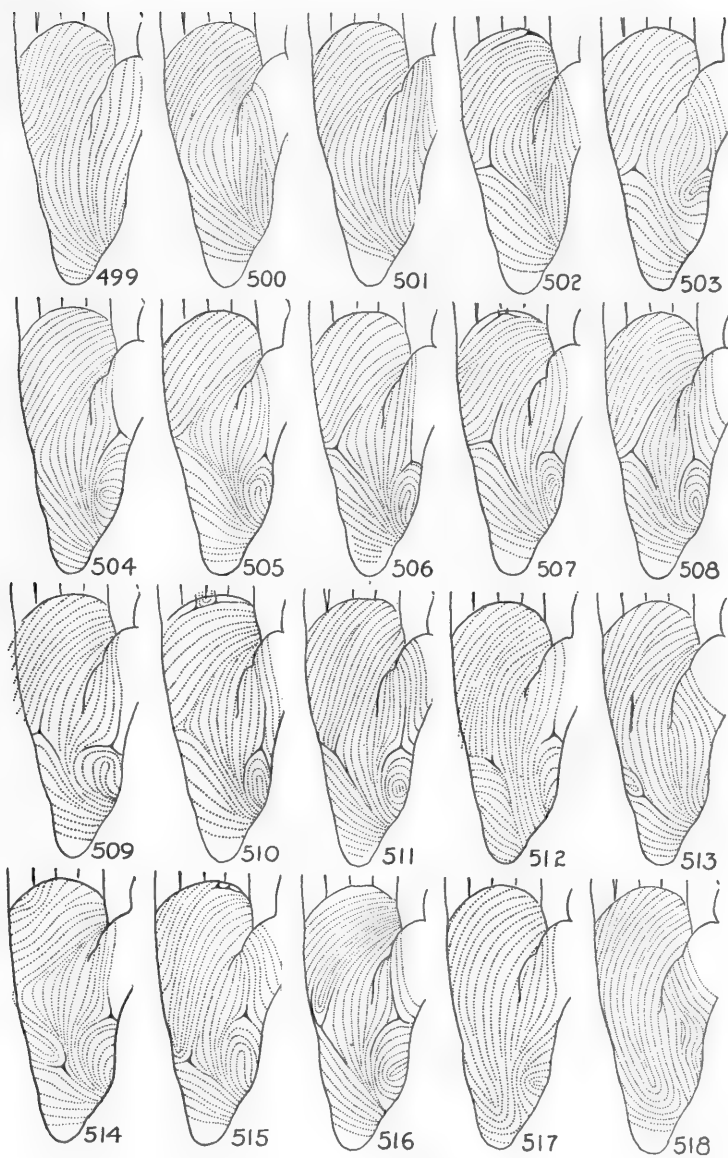
I (45): O (45).

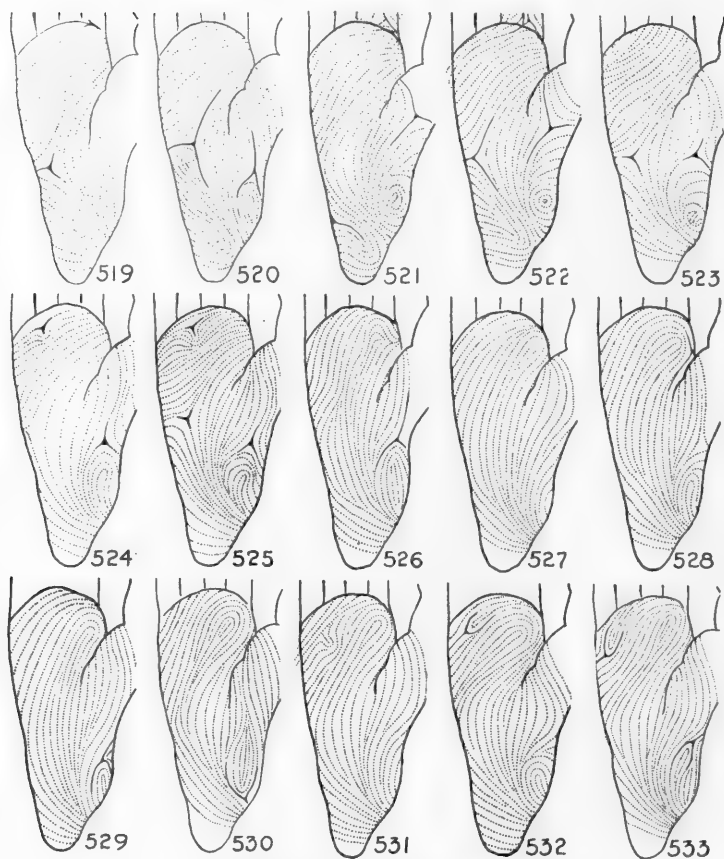
II (46): O (37); V (1); L<sup>p</sup> (8).

III (46): O (42); T (2); L<sup>p</sup> (2). The L<sup>p</sup> configurations have been counted in association with both II and III, since the patterns are broadened to extend into area II.

IV (45): O (38); V (2); T (2); L<sup>d</sup> (2); L<sup>t</sup> (1). One of the tented arches is so placed as to be common to III and IV; it has been counted in association with both areas.

CA (45): O (45).

Figs. 499-518 *Hylobates*, pes.

Figs. 519-533 *Hylobates*, pes.

## SYMPHALANGUS

## Manus (3)

## Figures 534-535

H<sup>d</sup>: O (3).H<sup>p</sup>: V (1); L<sup>du</sup> (1); L<sup>r</sup> (1).

Th + I: O (1).

Th: L<sup>r</sup> (2).

I + Th: See above.

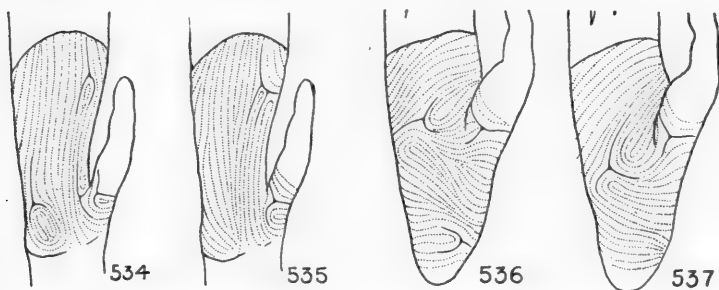
I: O (1); L<sup>d</sup> (1).

II: O (3).  
 III: O (3).  
 IV: O (3).  
 CA: O (1). 2<sup>p</sup>: L<sup>p</sup> (2).

Pes (15)

Figures 536-537

H<sup>d</sup>: O (15).  
 H<sup>p</sup>: O (2); V (1); L<sup>p</sup> (8); L<sup>t</sup> (2); S (1); L<sup>p</sup>L<sup>t</sup> (1).  
 C: O (4); V (1); L<sup>t</sup> (10).  
 Th: O (4); L<sup>p</sup> (5); L<sup>t</sup> (4); S (1); SL<sup>t</sup> (1).  
 I: O (9); L<sup>d</sup> (4); L<sup>p</sup> (1); L<sup>p</sup>V (1).  
 II: O (13); L<sup>t</sup> (1); L<sup>p</sup> (1). The L<sup>p</sup> pattern is counted with I as well as II since it is broadened to include both.  
 III: O (15).  
 IV: O (13); L<sup>d</sup> (1); L<sup>t</sup> (1).  
 CA: O (15).



Figs. 534-535 *Symphalangus syndactylus*, manus.

Figs. 536-537 Same, pes.

SIMIAE (ANTHROPOIDEA; SIMIANS)

CATARRHINAE

PONGIDAE (GREAT APES)

PONGO (ORANG; OURANG-OUTAN)

GORILLA (GORILLA)

PAN (CHIMPANZEE)

HOMINIDAE

HOMO (MAN)

(The term "higher primates" has been used to embrace Hylobatidae, Pongidae and Homo.)

## PONGO

## Manus

## Figures 538-549

In all the Pongidae the reliefs of the palm and sole closely resemble the human hand and foot with respect to faintness of pad indications, and in *Pan* the pads are almost totally suppressed.

(H, 17)  $H^d + H^p : L^p$  (2); S (8).

$H^d : O$  (7).

$H^p : L^p$  (1); W (1); S (5).

Th (19): Th + I: O (1);  $L^d$  (4).

Th: O (8);  $L^d$  (2);  $L^r$  (4).

I (19): I + Th: See above.

I: O (1); V (2);  $L^d$  (10); W (1).

II (19): O (5);  $L^d$  (11);  $L^p$  (1);  $L^dL^d$  (1);  $L^pL^d$  (1).

III (19): O (16);  $L^d$  (2);  $L^p$  (1).

IV (19): O (8); V (1);  $L^d$  (9);  $L^dL^r$  (1).

CA (19): O (16).  $2^p : V$  (1).  $3^p : V$  (1). P-th:  $L^d$  (1).

## Pes

## Figures 550-559

(H, 20)  $H^d : O$  (18);  $L^r$  (2).

$H^p : O$  (19); T (1).

C (20): O (3); V (5); T (1);  $L^r$  (4);  $L^t$  (2); W (2); S (3).

Th (20): O (3);  $L^t$  (16); W (1).

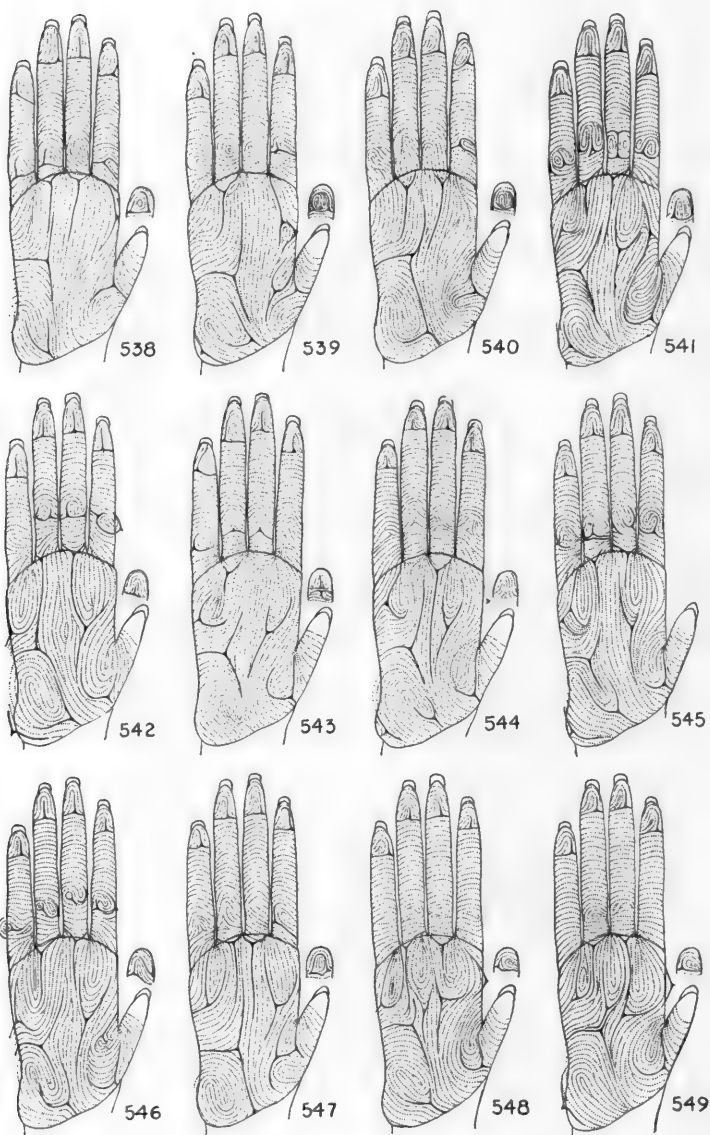
I (20): O (17);  $L^d$  (3).

II (20): O (7); V (4);  $L^r$  (1);  $L^p$  (6); S (1);  $L^pL^p$  (1). The  $L^pL^p$  pattern is broadened into the area of III and is counted as both II and III.

III (20): O (12);  $L^d$  (3);  $L^p$  (1);  $L^pL^p + II$  (1);  $L^d + IV$  (2); W + IV (1). The expanded patterns in the last 3 notations are counted also with the areas indicated.

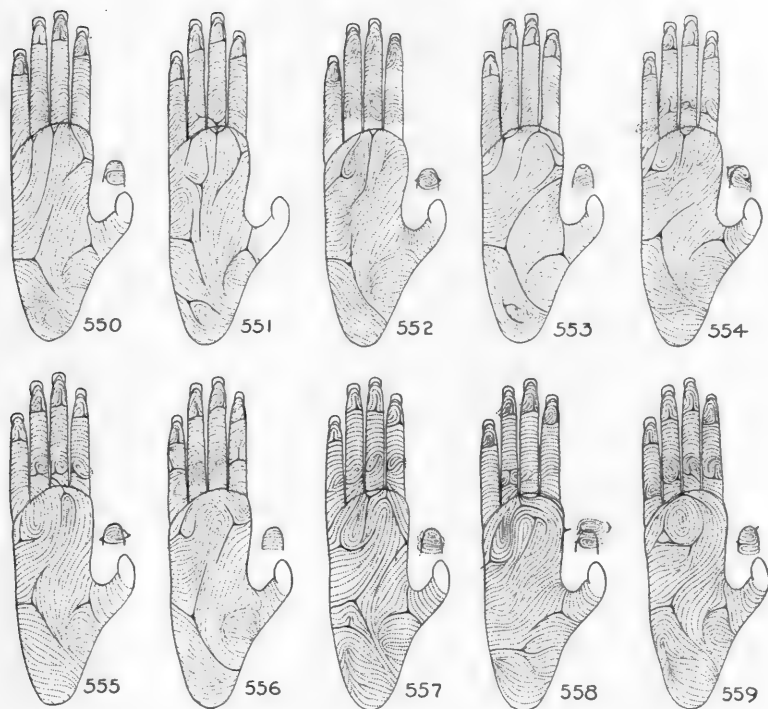
IV (20): O (10);  $L^d$  (7);  $L^d + III$  (2); W + III (1).

CA (15): O (13).  $4^p : W$  (1);  $L^tL^r$  (1).



Figs. 538-549 *Pongo pygmaeus*, manus.





Figs. 550-559 *Pongo pygmaeus*, pes.

### Supplementary note

After completion of this study seven additional hands and seven feet were loaned us by Dr. A. H. Schultz (field numbers from the Asiatic Primate Expedition of 1937: 261, 262, 277, 355, 380, 393, 444 — one hand and one foot of each animal). The dermatoglyphics have been analyzed by the procedures followed in the other material; since the features conform to those which had been recorded in detail it is deemed unnecessary to reproduce them as drawings or to incorporate the findings in tabulations.

## GORILLA

## Manus (11)

## Figures 560-568

$H^d + H^p$ : O (1); W (1); S (2).

$H^d$ : O (1); V (1);  $L^p$  (5).

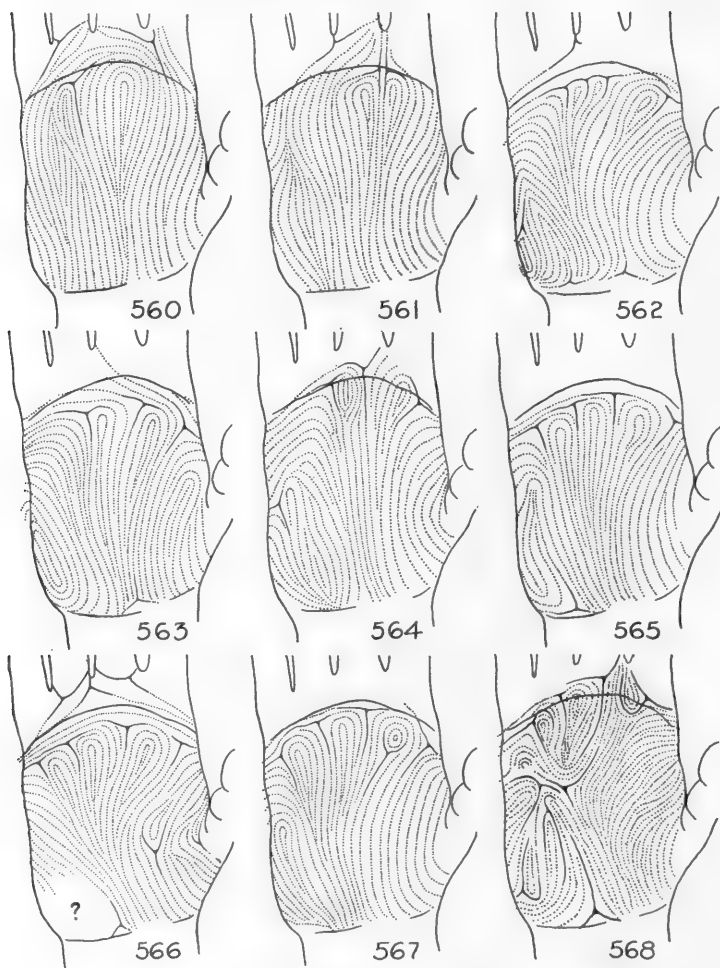
$H^p$ : O (3);  $L^d$  (3);  $L^a$  (1).

Th + I: O (6);  $L^p$  (1).

Th: O (3);  $L^d$  (1).

I + Th: See above.

I: O (1); V (1);  $L^d$  (1);  $L^p$  (1).



Figs. 560-568 Gorilla, manus.

II:  $L^d$  (1);  $L^p$  (7);  $L^p + III$  (1); W (1);  $L^p L^p$  (1).

III:  $L^p$  (8);  $L^p + II$  (1); W (1);  $L^p L^p$  (1).

IV: O (3);  $L^p$  (8).

CA: O (9).  $2^p$ :  $L^d$  (1).  $4^p$ : V (1).

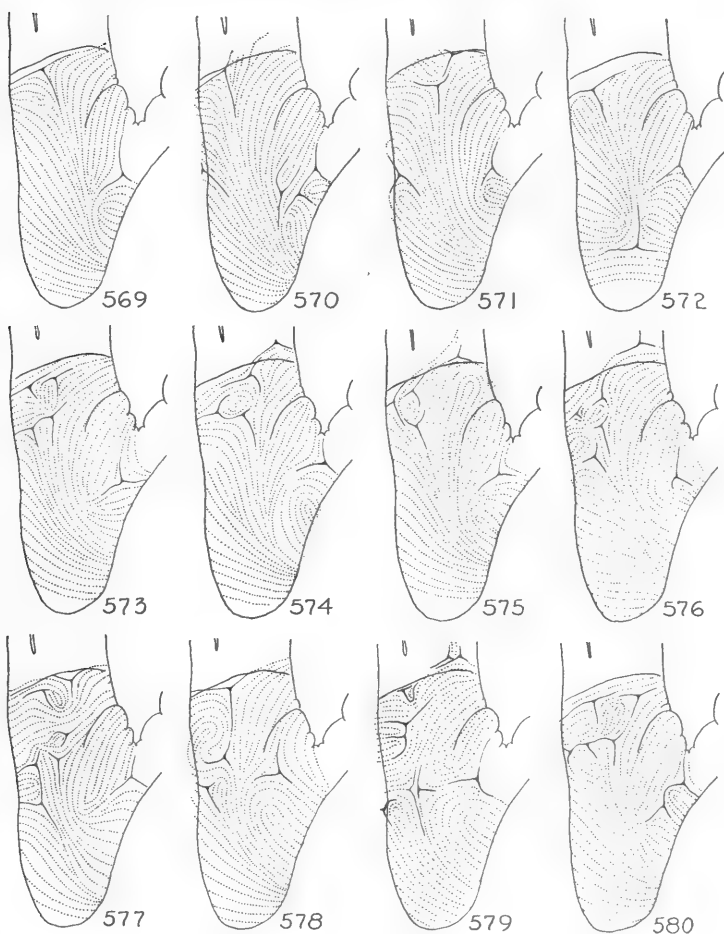
Pes (17)

Figures 569–580

$H^d$ : O (6); V (1);  $L^f$  (2);  $L^p$  (4);  $L^t$  (1); S (3).

$H^p$ : O (11);  $L^f$  (1);  $L^p$  (3);  $L^t$  (2).

C: O (15);  $L^t$  (1);  $L^p L^t$  (1).



Figs. 569–580 Gorilla, pes.

Th: O (5); L<sup>p</sup> (2); L<sup>t</sup> (8); S (2).

I: O (6); L<sup>d</sup> (10); L<sup>p</sup> (1).

II: O (16); L<sup>p</sup> (1).

III: O (9); V (1); L<sup>d</sup> (1); W (3); S (3).

IV: O (7); V (3); L<sup>d</sup> (1); L<sup>t</sup> (2); L<sup>p</sup> (1); W (2); S (1).

CA: O (17). While it is possible that features which appear to lie in 3<sup>p</sup> (figs. 573, 577, 580) should be identified with the distal central area, they seem to be more closely related to H<sup>d</sup>, with which they have been counted.

#### PAN

#### Manus

#### Figures 581-583

(See also Cummins and Spragg, figs. 1-20.)

(H, 79) H<sup>d</sup> + H<sup>p</sup>: O (35); L<sup>p</sup> (5); L<sup>u</sup> (1); S (1).

In addition there is one palm presenting the unusual combination of an L<sup>p</sup> situated in the mid-ulnar level, accompanying a W in H<sup>p</sup>, the W being counted below with H<sup>p</sup>; all other patterns representing H<sup>d</sup> + H<sup>p</sup> are the only patterns of the hypotheneal territory.

H<sup>d</sup>: O (32); L<sup>p</sup> (3); L<sup>r</sup> (1).

H<sup>p</sup>: O (1); L<sup>d</sup> (31); L<sup>p</sup> (3); W (1); S (1).

Th (80): Th + I: V (5); L<sup>d</sup> (4); L<sup>r</sup> (2); T (4).

Th: O (41); L<sup>r</sup> (23); W (1).

I (80): I + Th: See above.

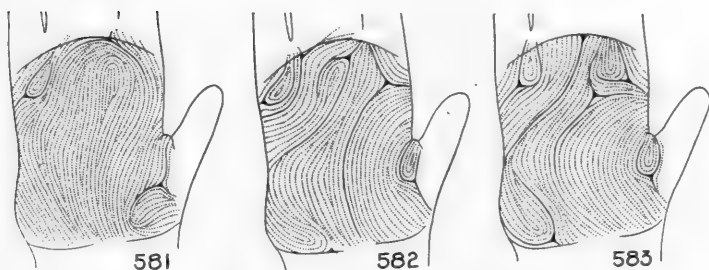
I: O (40); V (5); T (1); L<sup>d</sup> (17); L<sup>u</sup> (1); W (1).

II (81): O (35); V (1); L<sup>d</sup> (4); L<sup>p</sup> (26); L<sup>p</sup> + III (5); W (4); S (6).

III (80): O (61); L<sup>p</sup> (12); L<sup>p</sup> + II (5); L<sup>u</sup> (1); W (1).

IV (80): O (31); L<sup>d</sup> (45); W (2); TL<sup>d</sup> (2).

CA (80): O (80).



Figs. 581-583 Pan, manus.

## Pes

## Figures 584-586

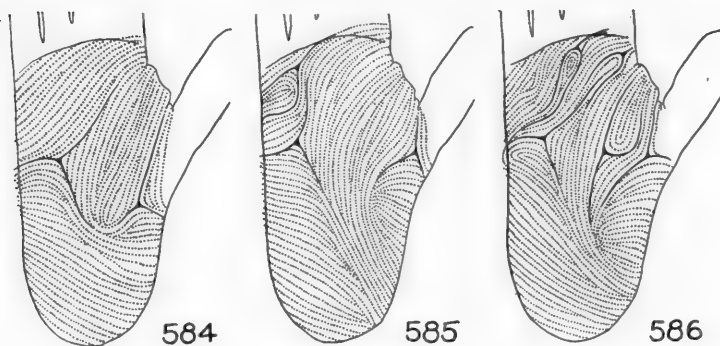
(See also Cummins and Spragg, figs. 21-40.)

(H, 65)  $H^d + H^p$ : T (3);  $L^t$  (11). $H^d$ : O (22);  $L^d$  (2);  $L^f$  (7);  $L^p$  (6);  $L^t$  (10); W (4). $H^p$ : O (46); T (2);  $L^t$  (3).

C (64): O (64).

Th (64): O (15); T (2);  $L^t$  (43);  $TL^t$  (1);  
 $L^tL^t$  (3).I (64): O (49); V (1); T (1);  $L^d$  (12); W (1).II (64): O (53);  $L^f$  (5);  $L^p$  (1);  $L^t$  (5).III (64): O (58);  $L^d$  (2);  $L^f$  (2);  $L^t$  (1);  $L^dL^f$  (1).IV (64): O (35); V (1);  $L^d$  (6);  $L^f$  (12);  $L^p$  (1);  
W (9).

CA (64): O (64).



Figs. 584-586 Pan, pes.

## HOMO

The palmar dermatoglyphics are tabulated from four racial series of unlike size: Germans, Cuban negroes, Comanche Indians, and Eskimos. The stated frequencies are direct averages of the percentages obtained in respective collections, not their weighted averages. Data for the plantar dermatoglyphics (excepting the thenar, as explained below) are obtained from four other collections, similarly combined: European-Americans, Jews, North American Indians and Liberian negroes. In the instance of the plantar hypothenar only the first two of these series are represented. A series of prints of the plantar thenar area alone was prepared especially for the present study. These prints were obtained from fifty male negroes, and the region printed conforms to the thenar area as defined by Wilder ('16).

In view of the large number of human subjects the frequencies of configuration types are stated in percentages.

## Manus (1176)

## Figures 587-589

H<sup>a</sup>: O (100.0).

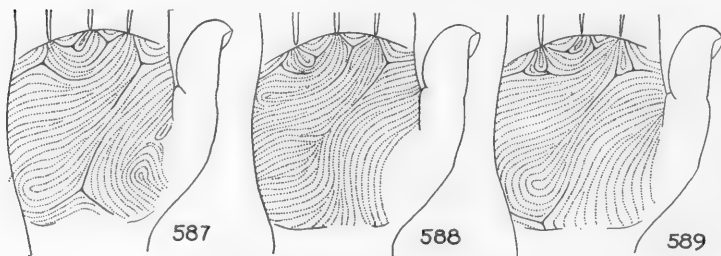
H<sup>p</sup>: O (74.3); V (1.0); L (22.2); W (1.2); S (1.4).

Th/I: O (82.9); V (8.0); L (2.6); LL (6.7).

II: O (93.0); V (2.4); L (4.8).

III: O (57.1); V (6.5); L (36.2); W (0.5).

IV: O (35.3); V (8.1); L (52.3); W (0.4); LL (4.0).

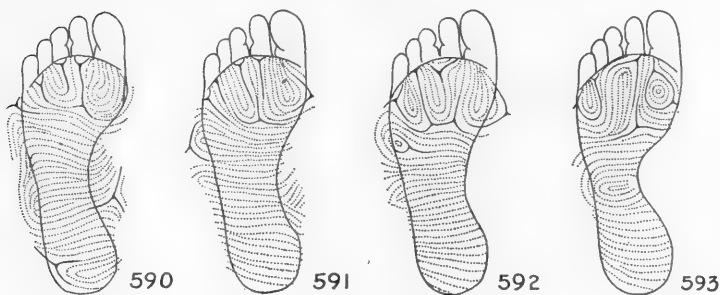


Figs. 587-589 Homo, manus.

## Pes

## Figures 590-593

- (H, 400)  $H^d + H^p$ : V (1.0); L (4.0).  
 $H^d$ : O (9.3); V (38.3); L (47.5).  
 $H^p$ : O (86.3); V (3.5); L (5.3).  
C (1212): O (99.2); L (0.8).  
 $Th^p$  (100): O (69.0); V (22.0); L (9.0).  
 $Th^d + I$  (1212): O (5.9); L (57.4); W (36.7).  
II (1212): O (67.4); L (29.8); W (2.8).  
III (1212): O (27.7); L (56.5); W (15.6).  
IV (1212): O (78.6); L (20.8); W (0.6).



Figs. 590-593 Homo, pes.

## DEPARTURES FROM THE BASIC PLAN

## VOLAR PADS

In a preceding section the morphologic plan of volar pads is described, and the nature of certain departures therefrom is suggested. Individual pads may be completely or partially suppressed, a pad may be expanded, two or more adjoining pads may be fused; also, there are marked variations in elevation and definiteness of circumscription. Most genera attain what may be termed a stable non-conformity to the plan, in that the pads of one or more regions present consistent departures. The ontogenetic fusion of originally discrete interdigital pads of the cat has been observed by Wilder (1897), and the drawings of fetal *Tarsius* in the Normentafel of Hubrecht and Keibel suggest a similar history in this animal of the plantar interdigital pads II and III.

*Palm.* In general, interdigital pads II, III and IV are the least subject to aberrancies. They are individually recognizable throughout the scale of primates, though markedly lowered in Ateles, Hylobatidae, great apes and man.

Interdigital pad I is frequently blended with the thenar pad to form a single prominent elevation, as described below. Pad I is separate in Tarsius, Lemur, Callithrichidae, Alouatta, Aotus and Ateles.

As just noted, the thenar pad and I are infrequently separate. Except in the genera named above, the two pads are fused, either lowered and melted together in one flattened expanse (the higher primates) or joined in a single prominent elevation (all prosimians except Tarsius and Lemur, all platyrrhines except Callithrichidae, Alouatta, Aotus and Ateles, and all catarrhine monkeys). When there is but one prominently elevated pad representing both these elements its summit usually is centered in I, the region of Th forming the extended proximal slope of the pad.

Hypothenar pads also are variable. There is a single elevation, H, in prosimians with the exception of Lemur, and in Saimiri. In all monkeys except Saimiri and in Hylobatidae there is a distinction between the two elements,  $H^d$  and  $H^p$ .  $H^p$  is generally prominent, while the  $H^d$  area is much lower or even markedly flattened. In this relationship  $H^d$  and  $H^p$  may be considered fused, with  $H^p$  in the ascendancy; the anatomical direction of ascendancy is the reverse of that in fusions of Th and I. In great apes and man the hypothenar pads participate in the flattening which is characteristic of other pads in these higher primates. Still, there are slight indications furnished by the hypothenar reliefs, even in their reduced state, reflecting superiority of  $H^p$  over  $H^d$ . These bare suggestions have greater significance when they are considered in company with the dermatoglyphics, which unquestionably evidence that tendency.

*Sole.* The greatest relative prominence and distinctness of pads II, III and IV occurs in prosimians. Catarrhine monkeys are characterized by well developed pads in this distal border



region, while platyrrhines evidence a lowering of the interdigital pads, carried to extreme degree in *Ateles*, *Lagothrix* and, to a lesser extent, in *Cebus*. In this respect the three genera named approach the conditions noted in *Hylobatidae*, great apes and man.

Pads Th and I are separate and distinctly elevated in all prosimians except *Nycticebus*, where they are joined in a common prominence as described above in palms. The *Callithrichidae* present in this region a narrow bolster, flattened on the surface, representing a fusion of Th and I. The only sign of division of this elongated eminence, apart from the dermatoglyphic expressions of its duality, is that it is cleft transversely by a flexion furrow. The thenar pad in *Aotus* is elongated and sometimes independent of I (fig. 2). In other platyrrhines and in catarrhine monkeys Th and I are separate, though Th is lowered and occasionally completely suppressed. The *Hylobatidae*, *Pongidae* and *Homo* show flattening and loss of individuality of the two pads.

Plantar hypothenar pads present the following variants. In *Nycticebus*, *Perodicticus* and *Galago* there is a single elevation, more or less rounded, with no indication of two components. *Tarsius* presents an elongated pad which fuses distally with pad IV and proximally with Th. This bolster-shaped pad is evenly elevated throughout its length, and is devoid of signs distinguishing  $H^d$  and  $H^p$ . In *Callithrichidae*, *Saimiri* and *Aotus* there is likewise a single elongated H pad, elevated as a ridge and without indications of  $H^d$  and  $H^p$ . In the simians not listed above, and in *Lemur*, the H area is elongated, lowered and flattened. There is often a suggestion of  $H^d$ , evidenced as a slightly more elevated region; its nature as an expression of  $H^d$  is corroborated by the dermatoglyphics.

*Accessory border pads.* Only in *Aotus* are pads  $II^r$  ( $II^t$ ) and  $IV^a$  ( $IV^t$ ) distinctly separated from the respective adjoining interdigital pads II and IV. Even in this genus the four pads are not consistently present,  $II^r$  being the least common.

In Callithrichidae the soles exhibit a separate II', somewhat displaced proximally in association with elongation of the sole. The accessory border pads in all other genera are either absorbed by the adjoining interdigital pads (notably in catarrhine monkeys) or they are so depressed that their existence is demonstrable only in the fetus (man, Cummins, '29) or in dermatoglyphic evidences.

*Central pads.* The central pads (2<sup>p</sup>, 3<sup>p</sup>, 4<sup>p</sup>) are located just proximal to the respective interdigital pads (II, III, IV). They are confined to prosimians and platyrrhines, but are neither consistently present in all members of these groups nor is the series fully represented in all the genera which possess these features.

Aotus may be selected as a primitive example of the central pads (figs. 1 and 2). Both in the hand and foot all three pads of the series are characteristically present as distinctly circumscribed elevations. While all these pads are typically present in hands and feet of the following genera they are lowered, expanded and less discrete than in Aotus: Leontocebus, Oedipomidas, Callithrix, Alouatta, Saimiri and Lagothrix. In Cebus the pads are present in the hand, but not in the foot, while in Seniocebus it is the foot alone which bears these pads. In four of the prosimian genera studied (Daubentonia, Nycticebus, Galago and Lemur) the central pads are indicated, and in no member except the hand and foot of Daubentonia and the hand of Lemur is the complete series even suggested. Central pads are inconspicuous in the hand of Daubentonia, but in the foot all three appear as proximal extensions of the interdigital pads, though divided from them by the distal transverse flexion furrow. Lemur has no distinct central pads, but in their morphologic positions there are patches of ridged skin larger than those in other regions of the central area. In the hand 2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup> are lacking. Nycticebus shows pads 2<sup>p</sup> and 3<sup>p</sup> in both members, and, while small, each pad is a discrete element. In Galago only 2<sup>p</sup> is present.

It is evident that central pads reach their highest development in certain platyrrhines. This degree of development is not shared by all members of the group, which embraces variations from the diagrammatically complete expression of *Aotus* to the absence of central pads in *Ateles*. The prosimians are more erratic. Central pads are absent in *Tarsius* and *Perodicticus*, and only incompletely and imperfectly expressed in the other available genera. The absence of definable central pads in adult catarrhines and in some genera of the lower groups may be the result of ontogenetic regression. The published photographs of fetuses of a catarrhine monkey, *Pithecus* (Schultz, '37 b), and man (Cummins, '29) suggest the occurrence of ill-defined central pads in the hand; though completely suppressed in later development, their presence in the fetus of forms which as adults lack these pads is of interest. Their history is like that of the border pads in man, which subside and undergo more or less complete absorption into the general surface.

*Comparisons between palm and sole.* Interdigital pads II, III and IV tend to be more lowered in soles than in palms, though in those forms which present the most extreme lowering in palm and sole (*Ateles* and the higher primates) it would be difficult to establish the relative standing of hand and foot with respect to discreteness of pads. The hypothenar divisions,  $H^d$  and  $H^p$ , are more commonly separately recognizable in palms than in soles. In palms  $H^d$  is characteristically lowered, while in soles the dermatoglyphic indications and occasionally the pads themselves point to greater elevation in  $H^d$  than in  $H^p$ . Pads Th and I of the palm usually are fused, and when elevated in a common prominence the summit is almost invariably centered in I. Soles commonly present separate Th and I pads.

Direct observation of pads admits the generalization that in the adult the palmar pads are more conspicuous than are those of the sole, as stressed above in reference to pads II, III and IV. The dermatoglyphics provide a measure of the

state of pads in the fetus (see discussion) and on the basis of these signs it may be deduced that the fetal pads likewise reach higher development in the palm (with the noteworthy exception of man).

#### CONFIGURATIONAL FIELDS

It becomes important, having outlined departures from the basic plan observed in the volar pads, to make a similar survey of the several configurational fields. One expression of departure from the plan is the failure of the individual configurational fields to be separately recognizable. The loss of identity of an individual area may be brought about either by the blending of neighboring areas to form a single pattern or by the failure of boundaries between adjoining open fields. It should be clear that an open field having boundaries formed by triradii signifies the individuality of a unit in the morphologic plan as effectively as does the occurrence of a well developed pattern occupying the area. On account of frequent individual variations, which may lead to varying completeness of the basic plan among different individuals of the same genus, we can only present for each genus having such variability a characterization of its modal type. In *Ateles*, for example, the statement that  $H^d$  and  $H^p$  are separately recognizable applies to the majority of the palms, ignoring the fact that in others  $H^p$  is represented by a pattern lacking separation from an open field in  $H^d$ .

*Palm.* Separate expressions of  $H^d$  and  $H^p$  may be realized through the occurrence of two distinct open fields (occasional in man, represented by the formulation  $A^c$  — Cummins, '35 b), two separate patterns (as in figs. 243–248), or a pattern and an open field separated by a triradial boundary (as in fig. 547). The genera in which these two elements are predominately or at least often distinct are: *Tarsius* (where the fusion of  $H^d$  and interdigital IV represents another departure from the palmar plan; only in *Nycticebus* and *Nasalis* is a similar blending of  $H^d$  to be found, but here the fusion involves  $IV^a$  instead of IV proper), *Nycticebus*, *Lemur*, all New World

monkeys except *Seniocebus* and *Saimiri*, and, among the catarrhines, *Papio*, *Pithecus*, *Cercocebus*, *Colobus*, *Gorilla*. The genera in which separation of the two elements is evident only occasionally are: *Lasiopyga*, *Pygathrix*, *Symphalangus* and *Homo*. Another departure is the occurrence, in varying frequency, of a pattern in the  $H^p$  area which is not limited from an open field extended into  $H^d$  (as in fig. 589), occurring in: *Seniocebus*, *Oedipomidas*, *Callithrix*, *Aotus*, *Ateles*, *Cebus*, all Old World monkeys except *Cercocebus*, *Hylobatidae*, *Pan*, *Homo*. A reversal of this situation occurs in *Perodicticus*, where it is  $H^d$  instead of  $H^p$  which is patterned (figs. 25-26). Finally, there is the condition in which a pattern lies at an intermediate level (as in fig. 115) or in which there is a continuous open field (fig. 581) as an indication of more intimate fusion of  $H^d$  and  $H^p$ . Such configurations occur sporadically among genera in all the groups except Old World monkeys. With the exception of examples in this last category, it will be clear that the two elements of the hypothenar region are characteristically distinct, since their identities are topographically separable even in the absence of a boundary line between a pattern in one and an open field in the other.

The thenar and first interdigital areas call for joint discussion on account of their frequent merging. These two configurational fields are characteristically separate in prosimians, though in *Tarsius* and *Lemur* there are cases presenting departures of the types characterized below. In *Callithrichidae* they are invariably separate. Among the genera of *Cebidae* and catarrhines, as well as within a single genus, there is variable behavior of Th and I. In all these genera, excepting *Magus* (only two hands available) and *Erythrocebus* (six hands), at least some individuals present independent configurations of the two areas. Such independence varies in frequency among the genera, being especially common in *Alouatta*, *Aotus* and *Pygathrix*, where the majority of hands are so distinguished. In about half the hands in *Pithecus* and *Pan* Th and I are separate. Smaller frequencies of the condition occur in *Saimiri*, *Ateles*, *Cebus*,

Papio, Lasiopyga, Hylobates, Pongo, Gorilla and Homo. The most common form of blending of Th and I is shown in the occurrence of a pattern centered in the area of I, with its peripheral portion extended into the territory of Th (as in figs. 239-242). Together with this there are cases in which the pattern center is less definitely assignable to I, being situated far enough proximally to lie in a zone properly belonging to both Th and I, or in which there is a single continuous open field. Mergers of the two configurational fields may be regarded as characteristic in the genera having the majority of hands thus marked: Saimiri, Cebus, Papio, Lasiopyga, Erythrocebus, Hylobates, Pongo, Gorilla, Pan, Homo. Numbers amounting to about half the hands with blending of Th and I occur in Lemur, Pithecius and Pygathrix. Lesser frequencies occur in Tarsius, Alouatta, Aotus, Ateles and Lagothrix.

Interdigitals II, III and IV are the most constant of all configurational fields, in the consistency with which they may be made out as separate areas. The constancy of expression of individual configurational fields appears to be a mark of primitiveness. Primitiveness of these interdigital regions is further expressed in their general tendency to the formation of conspicuous patterns. The main irregularities are noted in Hylobatidae, where the open fields representing II, III and IV are commonly fused in the absence of limits provided by digital triradii. In Pan and Gorilla such fusions occur, though less frequently. With the small number of gorilla hands the relative frequency of this condition cannot be determined reliably, but the suggestion is that departures of this nature are less common than in Pan. The occurrence of fusions of configurational areas, virtually limited to the apes and man, is of importance in relation to the relatively low degree of pad development. As another expression of instability of the interdigital fields, noted especially in Gorilla (figs. 564, 568) and Pan, and more marked in the former, are slight but appreciable displacements of patterns from the

positions which have come to be regarded as typical centerings of configurational fields.

The accessory border fields  $II^r$  and  $IV^u$  are expressed in three different relationships. They may appear as patterns, or as discrete open fields separable from the adjoining border configurational areas, or they may be considered absorbed by expansion of these neighboring areas. Only in three genera is  $II^r$  in the form of a pattern, and that only as an occasional occurrence — *Aotus*, *Gorilla* and *Pan*. It is a separately recognizable open field especially in *Alouatta*, *Lagothrix*, *Gorilla*, *Pan* and *Homo*.  $IV^u$  is characteristically patterned in *Aotus*, and in *Gorilla* two of the eight hands are patterned. The area of  $IV^u$  is a separately defined open field especially in *Nycticebus*, *Lagothrix*, *Gorilla*, *Pan* and *Homo*. In all the remaining genera the expanse of interdigitals II and IV is such that they encroach on the areas of  $II^r$  and  $IV^u$ , which are thus absorbed either in a single open field or pattern. In *Nycticebus* and *Nasalis*  $IV^u$  is characteristically fused proximally with  $H^d$ .

Pattern elements in the distal portion of the central area ( $2^p$ ,  $3^p$  and  $4^p$ ) are characteristic in New World monkeys. *Aotus*, with all three of these elements commonly expressed (figs. 126–137), represents the extreme development of patterns in this region. Generally they are much less consistent in number, with only one or two of the patterns appearing in a single hand, and even this partial expression is not as frequent as in *Aotus*. Among the prosimians, *Nycticebus* occasionally exhibits such patterns, but it must be noted that while this region in the other forms does not present continuous epidermal ridges, there is a tendency especially in *Lemur* (*Mutrux-Bornoz*, pls. 4 and 7) toward more marked ridge formation in patches corresponding to the areas of  $2^p$ ,  $3^p$  and  $4^p$ . Patterns  $2^p$ ,  $3^p$  and  $4^p$  occur sporadically in some Old World monkeys (*Pithecus* and *Pygathrix*), and more commonly in *Hylobatidae* and in *Pongo*.

The parathenar region, lying in the proximal part of the central area, is separately definable in nearly all primates.

Its individuality is indicated by the absence of formed ridges in most of the prosimians, in *Aotus* and in *Nasalis*. A definite parathenar pattern is commonly present only in *Ateles* and *Lagothrix*; it occurs infrequently in *Alouatta*. In the absence of a pattern the parathenar area is usually evident as a more or less discrete open field lying between the thenar and hypothenar areas. This relationship is indicated in *Pongo* (figs. 538–549), but in other catarrhines the parathenar region may be absorbed by the expanded thenar and hypothenar configurations, whether patterns (as in figs. 237–248) or open fields (figs. 560–568).

*Sole.* As in the palm,  $H^d$  and  $H^p$  may be present as two separate elements or as one configuration. They are separate in half or more of the available soles of *Nycticebus*, *Pterodicticus*, *Galago*, *Oedipomidas*, *Saimiri*, *Aotus*, *Lagothrix*, *Cebus*, *Papio*, *Pithecus*, *Erythrocebus*, *Pygathrix*, *Hylobates*, *Pongo*, *Gorilla*, *Pan*. Fusions of  $H^d$  and  $H^p$  are represented by a single pattern situated at an intermediate level, a single pattern seated in  $H^d$  with its periphery blending into an open field in the  $H^p$  territory, or by a continuous open field extending over both regions. The genera in which half or more of the soles are characterized by one or another type of fusion of  $H^d$  and  $H^p$  are: *Tarsius*, *Lemur*, *Callithrix*, *Alouatta*, *Ateles*, *Pithecus*, *Lasiopyga*, *Erythrocebus*, *Hylobates*, *Symphalangus*, *Gorilla*, *Pan*, *Homo*. In *Tarsius* and *Gorilla* (one sole in each)  $H^d$  may fuse with IV, and in *Nycticebus* (two soles of six) there may be fusion with IV<sup>t</sup>. In all soles of *Tarsius* there is fusion of  $H^p$  and Th to form a continuous open field; while this does not differ fundamentally from the comparable continuity of open fields in some other genera, the topography of the V-shaped ridged area, enclosing the ridgeless parathenar region, is worthy of note.

In the material as a whole, excepting the prosimians, no question arises with regard to the reality of two thenar configurational units,  $Th^p$  and  $Th^d$ , but they exhibit so much variation even within the same genus that it is difficult to arrive at a statement of what constitutes their characteristic



relationship. In addition to the separate state of these configurational elements there are fusions manifested in two different ways: a continuous open field extending through both territories, without a separation or regional differences in ridge direction which would suggest two components; a single pattern centered in the interval between the sites of  $Th^p$  and  $Th^d$ . In the prosimians the morphology of the thenar region, with its single configuration, suggests a likeness to the nature of the palmar thenar field. Here, as in the palm, this single configuration may be interpreted as an elemental unit rather than as a fusion of two fields. Actually, of course, the thenar configuration in prosimians (as is true of the thenar in the palm) represents  $Th^d$  alone, the territory of  $Th^p$  not being extended proximally as a ridged area. Above the prosimians, the genera having half or more of the soles presenting separate  $Th^p$  and  $Th^d$  are: *Saimiri*, *Aotus*, *Cebus*, *Papio*, *Lasiopyga*, *Erythrocebus*, *Hylobates*, *Homo*. Fusions of  $Th^p$  and  $Th^d$ , combining both expressions mentioned above, occur in half or more of the soles of: *Callithrichidae* in general, *Alouatta*, *Saimiri*, *Ateles*, *Lagothrix*, *Pithecus*, *Symphalangus*, great apes.

Fusion into a single configurational field representing  $Th^d$  and I occasionally occurs. In some genera (*Ateles*, *Cebus*) the fusion takes the form of a continuous open field, while the probably more significant type of fusion (occurring rarely in *Papio*, more frequently in *Pithecus*, and almost universally in *Homo*) is in the form of one expanded pattern.

The interdigital patterns I, II, III and IV, as in the palm, are noteworthy for their rather consistent conformity to the morphologic plan. The departures which occur are fusions of adjacent configurational fields. Just as  $Th^d$  and I are occasionally blended, so sometimes are I and the central area, II and III, and III and IV. Interdigital I expands into the parathenar region of the central area when boundaries between them are lacking or shifted; this occurs frequently in *Hylobatidae* and *Pongidae*. Among the prosimians, blending the II and III is constant in *Tarsius* and occurs infre-

quently in *Nycticebus*. Among the New World monkeys it is seldom that fusions of II and III occur, though in *Cebus* about one-fifth of the soles show no digital triradii separating these areas when they are open fields. In the Old World monkeys also the interdigital areas are typically not fused; in *Pygathrix* fusions of II and III and of III and IV occur rarely. In the *Hylobatidae* there is characteristic blending of interdigitals II, III and IV. Gorilla and chimpanzee frequently exhibit this type of fusion; it occurs rarely in orang and in man.

The accessory border fields, II<sup>c</sup> and IV<sup>c</sup>, occur as patterns only in *Aotus*. In *Lagothrix* they are distinctly limited from the neighboring interdigital fields, though in no case is a pattern found in them. Elsewhere throughout the primate series the accessory border areas usually are absorbed by the neighboring interdigital areas, though occasionally their territories are indicated, in less marked degree than in *Lagothrix*.

Patterns in the distal portion of the central area (2<sup>p</sup>, 3<sup>p</sup> and 4<sup>p</sup>) are sporadically and variably expressed. The occurrence of vestiges and patterns appears to be characteristic in most New World monkeys (see especially *Aotus*, figs. 138-149), but only rarely in the other groups is there even a questionable suggestion of their presence.

The proximal part of the central area, the parathenar, exhibits wide variation among the genera and even among the individuals of the same genus. Some forms, including most of the prosimians and *Aotus*, lack ridges in this area. When the area is completely ridged it is seldom that a true pattern is formed (as in figs. 37, 40, 412, 426, 428). In the absence of a pattern the region may still be indicated, as it commonly is at least in some individuals of all the remaining groups. The parathenar area may be an open field distinguishable from the adjoining border areas only through differences in ridge direction (e.g., fig. 43). Its distinctiveness is usually heightened by the presence of bounding radiants associated with it and the neighboring border fields (see figs. 441-450). The parathenar area may be completely ex-

tinguished by absorption into expanded hypothenar and thenar patterns or by blending into their continuous open fields, this occurring characteristically in *Ateles*, *Lagothrix*, *Hylobates* and *Homo*. A fairly wide range of variation in the configuration of the parathenar area may be found in a single genus, e.g., *Lasiopyga*, figures 405-419.

The calcar configurational field is in the heel region. This region in prosimians is hairy and thus is not included in the zone of dermatoglyphics. In all other groups the calcar area is usually completely ridged, the configuration being either an open field or a pattern. Patterns occur inconstantly in those genera which bear them at all and these genera are scattered in the simians without relationship to the taxonomic groups. Genera in which calcar patterns are relatively very common, occurring in about half or more than half of the soles available, are: *Alouatta*, *Ateles*, *Symphalangus* and *Pongo*. Lesser but still significant frequencies occur in: *Callithrix*, *Saimiri*, *Cebus*, *Pithecus*, *Cercocebus*, *Hylobates* and *Gorilla*. In all other genera calcar patterns are either extremely infrequent (*Lasiopyga*, *Pygathrix*, *Homo*) or absent.

*Comparisons between palm and sole.* In comparing the departures from the morphologic plan in hand and foot the following trends of unlikeness between the members, in their homonymous areas, are to be especially emphasized. (1) In the hand, when  $H^d$  and  $H^p$  are represented by a single pattern, that pattern is most frequently situated in  $H^p$ . This is reversed in the sole, where if in such blendings the pattern does not lie at a level intermediate between the characteristic positions of  $H^d$  and  $H^p$ , it is usually in the  $H^d$  region. (2) Single hypothenar patterns lying at the intermediate level between  $H^p$  and  $H^d$  are characteristic of more genera in the case of the sole than of the palm. This placement of a hypothenar pattern may be regarded descriptively as a phase in the absorption of the two elements which, if carried to its full expression, might be evidenced as the combination having a pattern center shifted still farther, either to  $H^d$  or to  $H^p$ . (3) The palm does not possess an equivalent of  $Th^p$ . Separate occurrences of

Th<sup>p</sup> and Th<sup>d</sup> are frequent in the soles of some New World monkeys, though it may be recalled that fusion between them is common. (4) Fusion between Th<sup>d</sup> and I in the sole occurs occasionally, but with no approach to the regularity with which such fusions occur in the palm, especially in the catarrhines. (5) Fusions between interdigital configurational fields are more common in the sole than in the palm. Such fusions are distributed among diverse groups, though occurring infrequently except in higher primates; in the palm they are confined to the higher primates.

*Comparisons among groups of primates.* Difficulties arise in the endeavor to convert the evidences of deviation from the basic plan into quantitative terms; additionally, the numbers available in some genera are too small to provide for a fully satisfactory analysis. There may be made, notwithstanding, certain general statements which apply to the main border pads, seven in the palm, eight in the sole. The prosimian genera are widely variable with respect to the extent of deviation from the plan. Nycticebus, Perodicticus, Galago and Lemur present the least departures, while Tarsius shows much more modification, especially in the foot. In this as in other analyses the prosimian genera are shown to be heterogeneous. Setting the group aside because of such peculiarities, the order of increasing tendencies to deviate from the plan is: New World monkeys, Old World monkeys, higher primates. For the higher primates the following order of modification is resolved: Homo < Pongo < Gorilla < ?Pan < Hylobatidae.

#### GENERAL RIDGE COURSES

The next descriptive analysis involves consideration of the prevailing directions of ridges over the palm and sole, apart from the localized irregularities of areas which are patterned. In forms having very expanded patterns, for example Papio (figs. 237-260), the determination of prevailing ridge directions is complicated by the fact that the areas free from patterns are not only small, but probably influenced by their

conjunction with the pattern fields. The relationships are quite different in a form such as *Hylobates* (figs. 459-533), where with suppression of pattern development the ridges pursue consistent courses over large areas.

In spite of the difficulties which are introduced in many genera by the expanse of patterns, it is desirable that comparisons of general ridge courses be made. As an illustration of significances which may be attached to these general courses of ridges, reference may be made to the long recognized fact that in man the palmar ridge directions approach the transverse more closely in right hands than in lefts. In further illustration it may be mentioned that chimpanzee palms, notwithstanding their sharp differences in ridge direction as compared to man, display exactly the same tendency of distinction between right and left (Cummins and Spragg). In the present material an analysis so exacting as that carried out in man and chimpanzee is impossible. The following comments therefore are devoted to a much more general comparison of the trait among the main groups of primates.

In some prosimians the lack of complete ridge formation over the palm and sole precludes a determination of ridge courses. In the prosimian genera in which ridge directions can be interpreted the general course in the palm is longitudinal, while in the sole the courses are either longitudinal or but slightly slanted.

In New World monkeys the characteristic ridge direction, as previously observed by Schlaginhaufen in the sole alone, is longitudinal both in palm and sole. The exceptions (palms of *Ateles*, *Lagothrix* and *Cebus*) take the form of an area of transversely coursing ridges lying proximal to the interdigital patterns, and (as in soles of *Cebus*) of obliquely transverse ridges in the distal and proximal regions (the fibuloproximal coursing of Schlaginhaufen).

It is especially interesting to note that the exceptional state just mentioned in the palms of three New World monkeys represents the characteristic alignment in the palms of Old World monkeys, where the expansiveness of patterns restricts

the area through which these alignments may be traced. The nearly consistent combination of longitudinally coursing ridges in the central palm and transversely coursing ridges bordering the interdigital patterns may be regarded as a correlate of the extent and distribution of the pads which are so highly developed in this group.

The soles in Old World monkeys are quite variable among the genera with respect to ridge direction. At the one extreme the ridges may be transverse (as in *Papio*) and at the other longitudinal (as in *Colobinae*); intermediate slants are not uncommon either as a characteristic of an entire sole (*Pithecus*, *Lasiopyga*) or in combination with an area of longitudinal ridge direction in the same sole. Different soles of the same genus may show unlikenesses in general ridge direction.

In the *Hylobatidae* ridge courses of the palm are strictly longitudinal, and in the sole either longitudinal or slanted. The same description applies to *Pongidae* except that in *Pan* the palmar ridge courses may be either longitudinal or oblique. The characteristic ridge direction in the human palm is a combination of longitudinal and diagonal, while in the foot the configuration is transverse or on a slant closely approaching it.

#### CAUDAL DERMATOGLYPHICS

Of the monkeys possessing prehensile tails, confined to the New World group, there are three genera in which caudal dermatoglyphics occur. Wood Jones' ('29) description of *Lagothrix* would apply equally well to the tails of *Alouatta* and *Ateles*: "The tail is long, highly specialized as a prehensile organ and naked below on its terminal part. This naked portion of the tail is beset with papillary ridges extraordinarily like those upon the palmar surface of a human finger."

In *Alouatta* (five specimens) the ventral surface of the tail presents two series of ridges meeting at the midline to form a simple herringbone configuration; the ridges in each

lateral series are straight, slanting distalward from the midline at an angle of about  $45^{\circ}$ . At the tip of the tail (see Schlaginhaufen, fig. 119D) the configuration in some cases is disposed in a whorl-like system. These observations agree with the descriptions of Purkinje (his fig. 20), Klaatsch, Whipple and Schlaginhaufen.

The tail in *Ateles* exhibits a like configuration, conforming to the illustration in Purkinje (fig. 20).

*Lagothrix* (two specimens, figs. 594-595) differs from *Alouatta* and *Ateles* in two respects. The herringbone configuration is not constant, and in the margins of the ridged area true patterns are irregularly disposed.

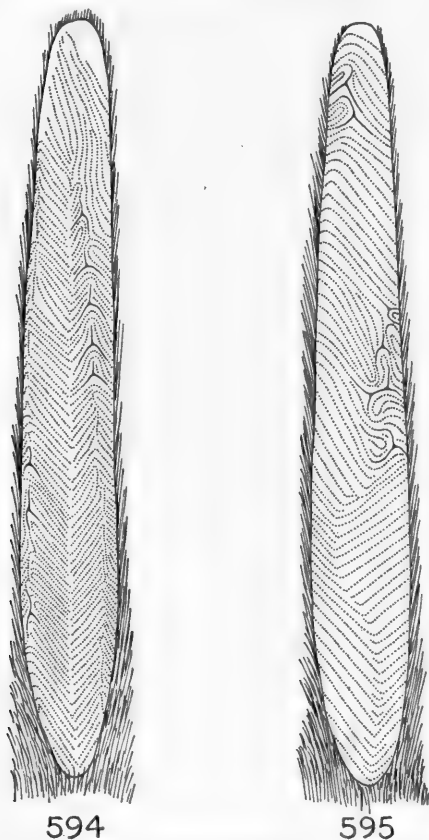


Fig. 594 *Lagothrix lagotricha*, dermatoglyphics on ventral surface of tail.  
Fig. 595 *Lagothrix infumata*, same.

Further consideration of the caudal dermatoglyphics depends upon an appreciation of the functions of the prehensile tail. Carpenter notes in *Ateles* the use of the tail not only in suspension but also in casting broken-off branches ('35), and the diverse uses of the tail in *Alouatta* ('34) are discussed in much greater detail, as follows.

"The tails of howler monkeys are always in use. During rest and sleep, the tail functions to anchor the animals to the branches of trees. After a young animal is about one month old it uses its tail to secure itself to its mother during rest as well as during locomotion, and this prehensile organ possibly accounts in part for the typical positions in which howler young are carried. The tail is used by resting animals to drive away flies and insects, and apparently as a currying or grooming organ, and I have seen both adult males and females manipulating their genitalia with the tip of the tail. During locomotion, this appendage functions as a grasping organ, and one which counteracts any tendency to fall. . . . The tails of monkeys vary greatly in degree of prehensiveness, and the howlers rank between capuchin and spider monkeys in this capacity. Capuchin monkeys have a semi-prehensile tail, whereas that of spider monkeys is extremely flexible and adaptive. The degree of prehensiveness is indicated by two things: (1) the proportion of the tail which is normally used for grasping, and (2) the arc through which the tail functions, if the point of attachment to the body is taken as a fulcrum about which the tail rotates. The grasping portion of howlers' tails roughly corresponds to the part of the tail which has a naked under skin. In an adult, this constitutes 20 cm., or about one quarter of the total length of the organ. . . . The prehensile tail is an organ of considerable importance in making possible the degree of arboreality found in howling monkeys."

Epidermal ridges, just as in the hand and foot, provide for increased security of grasp and heightened sensibility, which would be of service in the various functions indicated above.

The conditions existing in *Alouatta*, *Ateles* and *Lagothrix* may be regarded as the highest degree of specialization of the caudal skin. Less advanced specialization is to be seen in



*Cebus*, where the ventral surface of the tail presents scantier hair throughout the area corresponding to the dermatoglyphic region of the three genera just named. In the zone of scanty hair the skin surface may be readily observed, at least in the newborn specimen examined. This grasping surface is marked by a series of transverse skin folds which are progressively narrowed proximo-distally. These corrugations, in a newborn *Cebus* having a tail 19.5 cm. in length, are limited to the distal 7 cm., where they gradually diminish in breadth from 3 mm. to 1.5 mm. The grooves separating the corrugations extend to the lateral surface, becoming shallower until the corrugations and the grooves disappear at about the middle of that surface. In the ventral midline of about the distal half of the tail there is a continuous shallow sulcus.

It is to be emphasized that the transverse folds of the tail in *Cebus* are not homologues of epidermal ridges; they may be likened instead, both in anatomic and functional significance, to the bulges on the flexor surfaces of digits. It is apparent that the folds would be a mechanical aid in grasping, through yielding and adaptation to the contours of surfaces.

The longitudinal furrow in the midventral aspect of the tail, mentioned only in the instance of *Cebus*, occurs also in the tails of other forms, being a superficial indication of the interval between the caudal flexors. In the monkeys which bear caudal dermatoglyphics, the angle of the herringbone configuration is aligned more or less regularly in this furrow.

### PATTERN INTENSITY

The numerous illustrations of palms and soles (figs. 5-593) provide a record of descriptive variations of the dermatoglyphics, and the tabulations accompanying them stand as condensed descriptions. Such data, however, are not well adapted to the tracing of resemblances and differences among genera, between hand and foot and between right and left sides, as well as among the several configurational territories. Some quantitative approach more fundamental in nature than

the mere recording of configuration types and their frequencies must be provided if the desired comparisons are to be made. An earlier consideration of "pattern intensity" in connection with finger prints (Cummins and Goldstein, '32; Cummins and Steggerda, '35) suggests a similar analysis in the present study. The pattern intensity of these authors (like the comparable "Deltie" of Kirchmair and Poll, '36) is a measure of the degrees of pattern elaboration; arches, loops and whorls are assigned values (0, 1 and 2 respectively) which represent, roughly though it may be, the scale of increasing configurational complexity. Summated for the individual, or for right and left hands or for single digits, these values are useful for comparison of what is believed to be a fundamentally important trait of the dermatoglyphics. Though the present numerical evaluations of configuration types differ from those cited in the studies of human finger prints, the principle here adopted is the same, being directed toward rating the degrees of configurational complexity. In accord with this principle and as detailed below, weights or values are assigned the various configurations, recognizing in these numerical ratings the levels of elaboration of patterns. Such values of pattern intensity may then be appropriately summated and averaged for the various comparisons. Though an apparent weakness of the procedure is the arbitrary assignment of weights to the different configuration types, we have been repeatedly impressed in the course of this study by evidences of the substantial worth of the method.

In view of the existence of individual variations in pattern intensity, a reasonable number of individuals of each genus is requisite in drawing comparisons with the use of this measure. Adequate numbers are not available in all the genera which have been treated in the descriptions. Only twenty-four non-human genera (named in tables 4 and 5) are represented in the study of pattern intensity, and in some comparisons the number (see tables 7 and 8) is still further reduced.

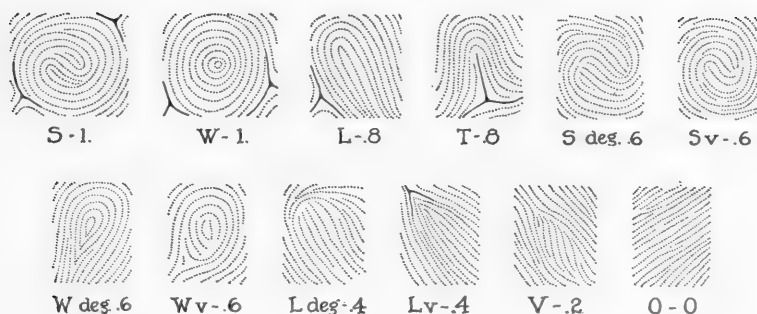


Fig. 596 Configuration types and their intensity values. Symbols of configuration types are explained in text.

A representative series of configuration types is shown in figure 596. The scheme of types is arranged in the order of diminishing pattern intensity, the values being indicated both in the figure and in the list which follows.

- 1.0 — whorls and S-patterns
- 0.8 — loops and tented arches
- 0.6 — degenerate and vestigial whorls and S-patterns
- 0.4 — degenerate and vestigial loops
- 0.2 — vestiges
- 0.0 — open fields.

Each of the border areas of the palm or sole ( $H^d$ ,  $H^p$ ,  $Th$ — $Th^p$  and  $Th^d$  in the sole — interdigitals I, II, III, and IV) is rated according to this scale of values. The accessory border elements ( $II^r$  and  $IV^u$  in the palm,  $II^r$  and  $IV^l$  in the sole), the central area ( $2^p$ ,  $3^p$ ,  $4^p$ , and  $P-th$ ), and calcar area are not included in the consideration of pattern intensity on account of the irregular occurrence of patterns in these regions. In both palm and sole there are occasional examples which call for special adaptation of the method as applied to the configuration of a single area. (1) Patterns in the hypothenar region which lie neither definitely in the distal nor proximal territory, but at an intermediate level, are assigned to  $H^p$ . (2) In the sole, because of the close association of  $Th^d$  and I, the two configurations are considered in common

under the heading of I; future references to Th in the sole thus apply to Th<sup>p</sup> alone. (3) Instances of a single pattern so expanded as to encroach into interdigital areas II and III are assigned to interdigital III.

### TOTAL INTENSITY

The expression "total intensity" applies to the sum of the intensity values of seven configurational areas: H<sup>d</sup>, H<sup>p</sup>, Th (representing Th<sup>p</sup> alone in the sole), I (including Th<sup>d</sup> in the sole), II, III and IV. Inasmuch as the maximum value for any single area is 1.00, the highest possible total intensity in a palm or sole is 7.00. This value has not been observed; its realization depends upon the appearance of a whorl or S-pattern in each of the seven configurational areas. For each genus total intensity is derived by averaging the total intensities of all the available individuals of that genus, palms and soles being treated separately. These values are listed in tables 4 and 5, and are recorded graphically in figure 597. To gain a concrete visualization of the descriptive import of the total intensity values, the illustrations of *Hylobates* (figs. 459-498) and of *Papio* (figs. 237-248) might be compared in the light of their contrasting total intensities, respectively 1.40 and 5.57.

Reference will be made repeatedly below to average pattern intensity values in non-human primates, abbreviated hereafter to "average". Averages are calculated, as in the consideration of total intensity, for twenty-three non-human genera, all being counted as of equal weight, notwithstanding that variable numbers of hands or feet are represented. The genera considered in the average are listed in tables 4 and 5. It should be noted here that *Colobus* and *Symphalangus*, which are respectively included in the averages of palm and sole, do not appear in all the following analyses for the reason that in neither case are hand and foot both represented adequately in our material.

Table 3  
Intermembral Indices:  
Pattern Intensity and Extremity Lengths

	$100 \times \frac{\text{Pattern intensity of palm}}{\text{Pattern intensity of sole}}$	$100 \times \frac{\text{Length of upper extremity}}{\text{Length of lower extremity}}$
Pongo	170	181
Cebus	168	128
Hylobates	143	157
	Average ----- 160	Average ----- 155
Gorilla	114	154
Pithecius	114	129
Alouatta	113	140
	Average ----- 114	Average ----- 141
Papio	108	132
Pan	102	147
Homo	45	108
	Average ----- 85	Average ----- 129

\* In fetuses: from Schultz - '26, '27, '37, '40 a.

Table 4  
Pattern Intensity in Palms

Number of palms	Genus	Total Intensity	H <sup>d</sup>	H <sup>P</sup>	Th	I	II	III	IV
8	Tarsius	0.76	.05	.23	.45	.00	.00	.00	.03
7-8	Nycticebus	4.52	.23	.63	.26	1.00	1.00	.40	1.00
3-4	Galago	6.10	.25	.95	1.00	1.00	.90	1.00	1.00
9-13	Lemur	4.75	.26	.83	.34	.48	.97	.89	.98
13-14	Oedipomidas	3.98	.29	.80	.55	.54	.69	.54	.57
4-5	Callithrix	3.83	.16	.76	.60	.56	.80	.30	.65
18-19	Alouatta	4.93	.15	.97	.60	.83	.71	.67	1.00
21	Saimiri	4.65	.05	.86	.09	.93	.93	.87	.92
13	Aotus	4.41	.00	.18	.37	.86	1.00	1.00	1.00
42-49	Ateles	3.49	.66	.84	.17	.41	.67	.04	.70
6	Lagothrix	4.50	.80	.83	.27	.70	.67	.40	.83
37-39	Cebus	4.49	.03	.93	.01	1.00	1.00	1.00	.52
23-30	Papio	5.57	.78	.88	.00	.96	1.00	.96	.99
86-91	Pithecius	5.46	.43	.91	.31	.87	.98	.96	1.00
4	Cercocebus	5.15	.50	.95	.00	.90	1.00	1.00	.80
17	Lasiopyga	5.13	.00	.91	.24	1.00	1.00	.98	1.00
6	Erythrocebus	4.73	.00	.80	.00	1.00	.93	1.00	1.00
15	Pygathrix	4.95	.33	.79	.45	.91	.83	.80	.84
5	Colobus	4.80	.16	.88	.36	.96	.92	.72	.80
44	Hylobates	1.40	.00	.84	.18	.35	.02	.00	.01
17-19	Pongo	3.01	.00	.96	.21	.68	.61	.11	.44
10-11	Gorilla	2.94	.35	.49	.07	.20	.44	.84	.55
79-80	Pan	2.06	.04	.31	.24	.33	.45	.19	.50
1176	Homo	1.14	.00	.21	.10		.04	.31	.48
	Direct average exclusive of Homo	4.16	.24	.76	.29	.72	.76	.64	.74

Table 5  
Pattern Intensity in Soles

Number of soles	Genus	Total Intensity	H <sup>d</sup>	H <sup>p</sup>	Th	I	II	III	IV
8-9	Tarsius	.22	.00	.00	.22	.00	.00	.00	.00
7	Nycticebus	2.96	.71	.11	.00	1.00	.54	.00	.60
4	Galago	5.25	.75	.25	.70	.90	1.00	.70	.95
11-14	Lemur	2.43	.11	.23	.14	.17	.55	.58	.65
13-14	Oedipomidas	2.70	.41	.00	.11	.48	.54	.36	.80
5	Callithrix	2.80	.52	.04	.60	.48	.64	.00	.52
22	Alouatta	4.35	.68	.11	.39	.89	.76	.56	.96
20-21	Saimiri	3.94	.25	.43	.52	.82	.55	.58	.79
12-13	Aotus	3.93	.40	.00	.60	.65	.85	.60	.83
33-34	Ateles	1.83	.35	.05	.26	.05	.29	.11	.72
5	Lagothrix	3.00	.56	.08	.36	.60	.24	.48	.68
35-36	Cebus	2.68	.39	.18	.24	.83	.05	.36	.63
24-28	Papio	5.14	.50	.42	.43	.94	.93	.98	.94
89-93	Pithecius	4.80	.76	.10	.63	.89	.79	.70	.93
5	Cercopithecus	5.56	.68	.84	.64	.84	.80	.96	.80
19	Lasiopyga	4.83	.45	.22	.41	.92	.88	1.00	.95
6	Erythrocebus	4.15	.53	.03	.13	.93	.87	.73	.93
14	Pygathrix	3.65	.83	.14	.37	.80	.49	.29	.73
45-46	Hylobates	.98	.04	.12	.56	.00	.11	.05	.10
15	Symphalangus	1.79	.00	.68	.61	.28	.11	.00	.11
20	Pongo	1.77	.08	.04	.63	.10	.34	.17	.41
17	Gorilla	2.57	.49	.28	.56	.45	.05	.36	.38
64-65	Pan	2.01	.37	.23	.63	.18	.14	.08	.38
400-1212	Homo	2.52	.46	.08	.10	.83	.27	.61	.17
	Direct average exclusive of Homo	3.19	.42	.20	.42	.57	.50	.42	.64

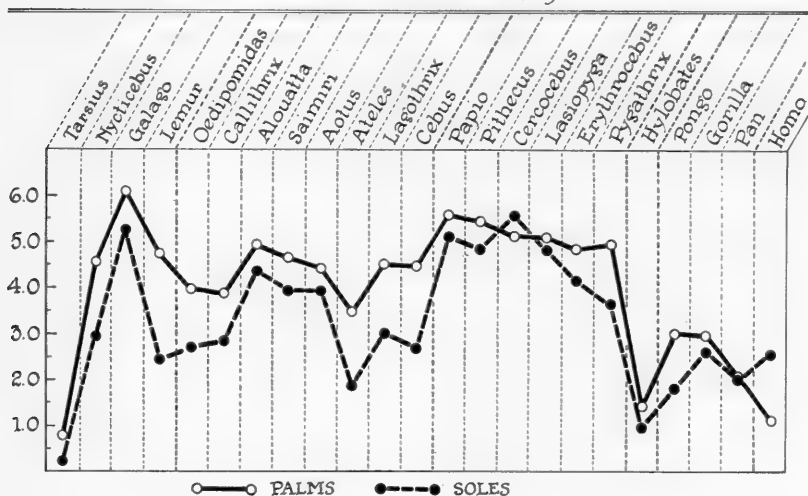
*Palm.* Total intensity values range from 0.76 to 6.10, with an average of 4.16. Man presents the value of 1.14, which is noteworthy in being one of the three lowest intensities; the minimum is in Tarsius, and in Hylobates the value is 1.40.

Of particular interest is the wide range of variation appearing in the four prosimian genera. It is here that the upper and lower limits of observed values occur (Tarsius, 0.76; Galago, 6.10), though in Nycticebus and Lemur the intensities (4.52 and 4.75 respectively) are not much above the average of non-human primates.

Compared to prosimians (exclusive of *Tarsius*), there is a drop in intensity in *Callithrichidae*, while with the exception of *Ateles* (3.49), the intensity values in other New World monkeys slightly exceed the average. In Old World monkeys the intensities are generally still higher. In *Hylobates*, as already noted, there is a low intensity value. In great apes are to be found consistently rather low values: *Pongo*, 3.01; *Gorilla*, 2.94; *Pan*, 2.06. The total intensity in man is 1.14.

*Sole.* The intensity values are almost invariably lower in soles than in palms, as shown in figure 597 and as indicated in the averages of the 23 genera — 3.19 in the sole as compared with 4.16 in the palm — and in the more limited range of plantar values.

Figure 597  
Total Pattern Intensity



The lower and upper extremes of total intensities in the sole are 0.22 and 5.56, though the only instances where the values are above 5.00 are found in *Cercocebus* (5.56), *Galago* (5.25), and *Papio* (5.14). Unlike the placing of *Homo* with reference to the palm, man is not included in the group of minimum intensities, though the value is low (2.52).

In prosimians, as was noted also in the palm, there is a wide range of variation: *Tarsius*, 0.22; *Nycticebus*, 2.96; *Galago*, 5.25; *Lemur*, 2.43. In *Callithrichidae* the values (*Oedipomidas*, 2.70 and *Callithrix*, 2.80) lie below the non-human average, while in other New World monkeys there are values both above and below the average, the least being that of *Ateles* (1.83) and the maximum that of *Alouatta* (4.35). All Old World monkeys have values above the average. In *Hylobates* the value is exceptionally low (0.98), though in the closely related *Symphalangus* the intensity rises to 1.79. Great apes show relatively low pattern intensity (*Pongo*, 1.77; *Gorilla*, 2.57; *Pan*, 2.01). The human sole has an intensity value of 2.52.

*Comparison of palm and sole.* Comparison of the total intensities of palm and sole in the same genus reveals, as just mentioned, an almost invariably higher value in the palm. Only *Homo* and *Cercocebus* are exceptions. Since in *Cercocebus* but four hands and five feet are available, observations in that genus are of slight weight. In man the reversal is significant in view of the large number of individuals represented. The exceptional status of man, total intensity of the sole (2.52) being greater than that of the palm (1.14), stands in suggestive relation to the sequence of intermembral differences in the great apes. The excess of hand over foot is progressively reduced in the order: *Pongo*, *Gorilla*, *Pan*. Palm and sole in *Pan* may be regarded as having equal intensities, since the difference is negligible. The great apes thus form a series indicating, in the order named, an approach to the human condition.

It was thought possible that the distinction between palm and sole with respect to total intensity might be associated in some way with other anatomical distinctions of the upper and lower extremities. Schultz supplies data on dimensional differences of the extremities in primates ('26, '27, '30, '37 a, '37 b, '40 a). Among his various dimensional records there is one determination presenting a suggestive relationship with pattern intensity. Data relating to nine genera meet the needs



of the comparison (table 3). The dimensional relationship in question is the intermembral index. We have made immediate uses of the intermembral index based upon total lengths of the extremities, though the indices involving humerus plus radius and femur plus tibia (Schultz, '30 and '37 a) are found to agree with the seriations of the higher primates now to be presented in terms of total lengths of the extremities. Since the intermembral index of extremity length diminishes in prenatal and postnatal development, it seemed most promising to inspect the indices which obtain at about the time of differentiation of the dermatoglyphics. The figures extracted from Schultz apply to fetuses corresponding to human gestation within the period comprising lunar months 4-6 inclusive; however, the seriations of the higher primates retain the same order, regardless of whether the intermembral indices are those of the fetal period or later. It will be noted (table 3) that all the higher primates — gibbon, the three great apes and man — are arranged in the same sequence, whether ordered according to the intermembral indices of total intensity or of dimensions. As for the other genera represented in the table, there is a less consistent seriation, and *Cebus* is the most conspicuous non-conformist in this series, having next to the highest pattern-intensity index of the nine genera and next to the lowest index of extremity lengths. The explanation of these discrepancies, which are in such contrast to the orderly behavior of the five genera of higher primates, can hardly be explained away on the assumption of a technical discrepancy, though it may be noted that the index of extremity lengths in *Cebus* is based on a single specimen, and that some fluctuation among individuals might be expected. Table 10 in Schultz ('26) lists the intermembral indices of extremity lengths in six age groups, three of them of the fetal period, and three groups of postnatal specimens, infant, juvenile and adult. While the general tendency of the index is to diminish with development, the progression, at least as indicated in those genera with larger number of specimens, is not uniform, the lack of uniformity being presumably associated with individual differences.

It seems hardly likely that the parallelism between the intermembral indices of pattern intensity and extremity lengths in higher primates is merely coincidental. The factor responsible for this association cannot be identified. It is possible, of course, that the growth rates which make for greater extremity lengths are in some way linked with those growth forces which condition pattern expression. This does not seem very plausible, on account of the discrepant placings of genera of monkeys in the seriation just presented. We have been considering the relative lengths of upper and lower extremities and the relative intensities of palm and sole without regard to the absolute values. *Hylobates*, for example, has a pattern intensity (combining palm and sole) which is just half that of *Pongo*, though the extremities in *Hylobates* are relatively much longer. Search for the explanation must be made elsewhere than in mere size, relative or absolute. It is not impossible that the correlation between differences in lengths of upper and lower extremities and in their pattern intensities are linked because of common locomotor habits. When the higher primates are listed in the order of decreasing arborealness (*Hylobates*, *Pongo*, *Pan*, *Gorilla*, *Homo*) the seriation does not correspond exactly to that based on the intermembral indices. At the same time, a precise conformity might not be manifested among features of the kinds here compared, especially when it is impossible to draw nice distinctions in functional use of the members. Making such allowances, there may be significance in the standing of *Pongo* and *Hylobates* at the top of all three lists; *Hylobates* is the more aboreal and the more active brachiator, but we cannot draw such fine distinctions in habit as in structural features which can be compared quantitatively. Man stands at the bottom of all three lists, and while the places of *Gorilla* and *Pan* are reversed in the order of decreasing arborealness as compared with their position based on the intermembral indices, the two genera at least lie in an intermediate position, and the remarks just made in reference to *Pongo* and *Hylobates* apply equally to them.

## REGIONAL PATTERN INTENSITIES

Attention may be next directed to the configurational areas individually. The values for both hand and foot, reduced to graphic form in figure 598, are listed in tables 4 and 5. This approach aims to disclose trends of variation in regional pattern intensity which might have phylogenetic implications or which might throw light on morphological questions, such as regulation of pattern intensity with reference to the anatomical axis, other gradients of pattern intensity, and bilateral asymmetry.

## INDIVIDUAL CONFIGURATIONAL FIELDS

*Palm.* In the *distal hypothenar* area ( $H^d$ ), the average pattern intensity is 0.24, the lowest value of any configurational field. In man  $H^d$  is so rarely patterned that only one example has been recorded previously (Cummins, '35 b, fig. 3); the second known example, obtained through the courtesy of Dr. D. C. Rife, is reproduced in figure 588. It is not surprising, accordingly, that the intensity value in our series of 1176 human hands is zero. Intensity is similarly at zero, or so close to it as to be negligible, in the following genera: *Tarsius*, *Saimiri*, *Aotus*, *Cebus*, *Lasiopyga*, *Erythrocebus*, *Hylobates*, *Pongo* and *Pan*. Notably high values occur in *Ateles* (0.66), *Lagothrix* (0.80) and *Papio* (0.78). Values ranging from 0.33 to 0.50 are noted in *Pithecius*, *Cercocebus*, *Pygathrix* and *Gorilla*. Values ranging from 0.15 to 0.29 occur in the remaining genera (*Nycticebus*, *Galago*, *Lemur*, *Oedipomidas*, *Callithrix*, *Alouatta*, *Colobus*).

The *proximal hypothenar* area ( $H^p$ ) exhibits a much higher average pattern intensity (0.76), this value not being exceeded in any other area, though equalled in interdigitals II and IV. The intensity of  $H^p$  is less variable among the genera than is  $H^d$ , as shown in figure 598. The highest values closely approach 1.00, while the lower values present the following noteworthy relationships. There is a progressive increase from *Tarsius* (0.23) to *Nycticebus* to *Galago* (0.95). *Aotus*



drops sharply to 0.18 and thus presents a singular low value in the midst of an otherwise consistent trend of high intensity to which all other monkeys adhere. Among the great apes a progressive drop in pattern intensity is to be noted in passing from Pongo (0.96) to Gorilla (0.49), to Pan (0.31), that drop being carried still further in man (0.21).

The *thenar* area (Th) presents an average intensity of 0.29. Fluctuations among the genera are marked, ranging from 0 to 1.00 and without orderly relations in the systematic groups.

In the *first interdigital* area (I) the average value is 0.72. The general trend of high intensity is broken by abrupt depressions in certain genera: Tarsius, 0; Lemur, 0.48; Oedipomidas, 0.54; Callithrix, 0.56; Ateles, 0.41; Hylobates, 0.35; Gorilla, 0.20; Pan, 0.33; Homo, 0.10. In man the true value would be less than 0.10, since in the routine formulation of human palms an exact distinction between Th and I often can not be made.

The *second interdigital* area (II) has an average value of 0.76. In keeping with this highest value of all interdigital areas, the majority of the genera show values of 1.00 or values not much below 1.00. Minimum intensities occur in Tarsius, 0; Hylobates, 0.02; man, 0.04. In great apes the pattern intensities, though below the average recorded for non-human primates, are much higher than in man: Pongo, 0.61; Gorilla, 0.44; Pan, 0.45.

The *third interdigital* area (III) presents the lowest average value of all the interdigital areas, 0.64. High values characterize Lasiopygidae and Cebidae, excepting Ateles (0.04) and Lagothrix (0.40). Callithrichidae have relatively low values (Oedipomidas, 0.54; Callithrix, 0.30). Prosimians and great apes are noteworthy for the dispersion of values within the groups. In prosimians the intensities range from 0 to 1.00, and in gibbon and great apes the intensities are: Hylobates, 0; Pongo, 0.11; Gorilla, 0.84; Pan, 0.19. The value in man is 0.31.

The *fourth interdigital* area (IV) has an average value of 0.74. Only Tarsius (0.03) and Hylobates (0.01) have values

indicating virtual suppression of patterns. Other values below the average are recorded for *Oedipomidas*, 0.57; *Callithrix*, 0.65; *Ateles*, 0.70; *Cebus*, 0.52; *Pongo*, 0.44; *Gorilla*, 0.55; *Pan*, 0.50; *Homo*, 0.48.

*Sole.* The pattern intensity of the *distal hypothenar* area ( $H^d$ ) averages 0.42. The lowest values occur in *Tarsius*, 0; *Lemur*, 0.11; *Hylobates*, 0.04; *Symphalangus*, 0; *Pongo*, 0.08. The intensities are consistently above the average in *Lasiopyginae* while the values in New World monkeys are variable, lying both below and above the average. Great apes show diversity: *Pongo*, 0.08; *Gorilla*, 0.49; *Pan*, 0.37. The value in man is 0.46.

The *proximal hypothenar* area ( $H^p$ ) has the lowest average value of all plantar areas, 0.20. The highest intensities are: *Saimiri*, 0.43; *Papio*, 0.42; *Cercocebus*, 0.84; *Symphalangus*, 0.68. Minimum values are noted in *Tarsius*, 0; *Nycticebus*, 0.11; *Oedipomidas*, 0; *Callithrix*, 0.04; *Alouatta*, 0.11; *Aotus*, 0; *Ateles*, 0.05; *Lagothrix*, 0.08; *Pithecius*, 0.10; *Erythrocebus*, 0.03; *Pygathrix*, 0.14; *Hylobates*, 0.12; *Pongo*, 0.04; *Homo*, 0.08. The remaining genera present values approximating the average.

The *thenar* area ( $Th$ ) has an average value of 0.42. Genera having pattern intensities considerably above average are: *Galago*, 0.70; *Callithrix*, 0.60; *Saimiri*, 0.52; *Aotus*, 0.60; *Pithecius*, 0.63; *Cercocebus*, 0.64; *Hylobates*, 0.56; *Symphalangus*, 0.61; *Pongo*, 0.63; *Gorilla*, 0.56; *Pan*, 0.63. The lowest values are in *Tarsius*, 0.22; *Nycticebus*, 0; *Lemur*, 0.14; *Oedipomidas*, 0.11; *Ateles*, 0.26; *Cebus*, 0.24; *Erythrocebus*, 0.13; *Homo*, 0.10. The remaining genera approximate the average: *Alouatta*, *Lagothrix*, *Papio*, *Lasiopyga* and *Pygathrix*.

With an average value of 0.57, the *first interdigital* area (1) presents next to the highest value of any area in the sole. In most of the non-human genera and in man the values lie well above the average, while the especially low values occur in *Tarsius*, 0; *Lemur*, 0.17; *Ateles*, 0.05; *Hylobates*, 0; *Pongo*, 0.10; *Pan*, 0.18.

The *second interdigital* area (II) has an average intensity of 0.50. The highest values occur in Galago, 1.00; Alouatta, 0.76; Aotus, 0.85; Papio, 0.93; Pithecius, 0.79; Cercocebus, 0.80; Lasiopyga, 0.88; Erythrocebus, 0.87. Low values occur in Tarsius, 0; Ateles, 0.29; Lagothrix, 0.24; Cebus, 0.05; Hylobates, 0.11; Symphalangus, 0.11; Pongo, 0.34; Gorilla, 0.05; Pan, 0.14. The remaining non-human genera approximate the average value, while man presents a relatively low intensity, 0.27.

The *third interdigital* area (III), with an average of 0.42, shows the highest intensities in Lasiopyginae and in Galago, ranging from 0.70 to 1.00. Extremely low values are to be found in Tarsius, 0; Nycticebus, 0; Callithrix, 0; Ateles, 0.11; Hylobates, 0.5; Symphalangus, 0; Pongo, 0.17; Pan, 0.8. Man presents the high value of 0.61.

The average value for the *fourth interdigital* area (IV) is 0.64, the highest of the plantar areas. Very low pattern intensity is found in Tarsius, 0; Hylobates, 0.10; Symphalangus, 0.11. With the exception of great apes (Pongo, 0.41; Gorilla, 0.38; Pan, 0.38), all other non-human genera show a high pattern intensity. In man the intensity value is low, 0.17.

*Comparison of palm and sole.* The reversal of intermembral relations of pattern intensity in man as compared to non-human primates, total intensity being greater in the human sole than in the palm, calls for intermembral comparisons of intensities in single configurational areas.

As shown in figure 598 there are two areas ( $H^d$  and  $Th$ ) which in the non-human forms are exceptions to the rule of higher pattern intensity in the hand, though in neither case is that exception consistent throughout the series of genera. Likeness of intensity values in corresponding configurational areas in the hand and foot of the same genus is especially evident in the interdigital series, most marked in IV, less so in II and III. In figure 598 it will be noted that palm and sole in the succession of genera tend to rise or fall together in pattern intensity, hence giving a general effect of parallelism even in those areas presenting wide differences in the absolute

values. The following areas are responsible for relative elevation of pattern intensity in the human sole:  $H^d$  and interdigitals I, II and III. The higher intensity in  $H^d$  of the sole is not exceptional, but the interdigital areas represent distinctive exceptions to the general trend in primates. In the instance of  $H^p$ , where the excess of hand over foot in pattern intensity is greater than in any other configurational area, mention must be made again of the relationship of the calcar region. If this region be regarded as a component of the plantar  $H^p$ , as suggested earlier in a consideration of its comparative morphology, its pattern intensity should be added to that of the plantar  $H^p$  for a just comparison with  $H^p$  of the palm. Even with this addition (not shown in fig. 598, which is concerned only with  $H^p$  as previously defined) the plantar pattern intensity remains lower than that of the palmar  $H^p$ .

#### INTERRELATIONSHIPS OF GROUPS OF CONFIGURATIONAL FIELDS

Having analyzed the intensities of individual configurational fields it is appropriate to combine certain of these fields in groups for determinations of collective regional variability. Two modes of grouping suggest themselves. The first mode involves two sets of configurational fields separated by the longitudinal axis (the thenar and hypothenar groups, as characterized next below). The second grouping divides three sets of configurational fields transversely (the distal, intermediate and proximal groups which are later considered).

Whether in palm or sole, the thenar and first and second interdigital areas comprise a series which is named the *thenar group*, situated on the radial or tibial side of the axis. On the opposite side of the palm or sole, ulnarward or fibularward from the axis, there is the *hypothenar group*, comprising the proximal and distal elements of the hypothenar configuration and the fourth interdigital area. Justification for the groupings chosen is afforded not only by the relationships to the anatomical axis but also by manifestations in some mammals that the pads are thus actually interrelated as



Figure 599

## Principle of Serial Comparisons of Digits and Interdigital Areas of Hand and Foot

	.90	.85	.80	.91	.84	Fingers
I	II	III	IV	V		
Toes	.80	.78	.91	.77	.45	
	I	II	III	IV	V	

A. *In man*: digital lengths, pattern intensity in apical patterns, localization of maximal frequency of radial (tibial) loops, and common localization of syndactyly. (The numbers inserted represent pattern intensities in Newman's series of fingers and toes.)

	3.8	30.8	44.2	21.2	Fingers
II	III	IV	V		
Toes	32.6	45.4	20.5	1.5	
	II	III	IV	V	

B. *In man*: retention of hair on middle segments of digits. (Danforth)

	.04	.31	.48	Palm
II	III	IV		
Sole	.27	.61	.17	
	II	III	IV	

C. *In man*: pattern intensities of interdigital areas.

	.76	.64	.74	Palm
	II	III	IV	
Sole	.50	.42	.64	
	II	III	IV	

D. *In non-human primates*: pattern intensities of interdigital areas.

groups in the disto-proximal direction. Fusion of pads IV,  $H^d$  and  $H^p$  in the sole of *Tarsius* and other indications of intimate linear aggregations of these pads, with corresponding evidences involving Th, I and II, suggests a fundamental significance of such groupings. Even deeper structures associated with the pads may exhibit comparable relationships. The cartilage plates in *Myopotamus*, as described by Zuckerkandl ('06), are blended into two sets, a radial group and an ulnar group, corresponding to the thenar and hypothenar groups of configurations here presented.

Summating the regional pattern intensities representing each of these groups, comparisons are to be drawn first between the thenar and hypothenar groups in the same member. Comparisons are made in terms of the percentile relation of the intensity in each group to the intensity of the two groups combined, this last being an adjusted total intensity, differing from the total intensity previously considered in that interdigital III is excluded. In presenting these figures in graphic form (fig. 600), the differences between the percentile values of the thenar and hypothenar groups are plotted above the base line or below it in accordance with whether the excess is in the thenar group or in the hypothenar.

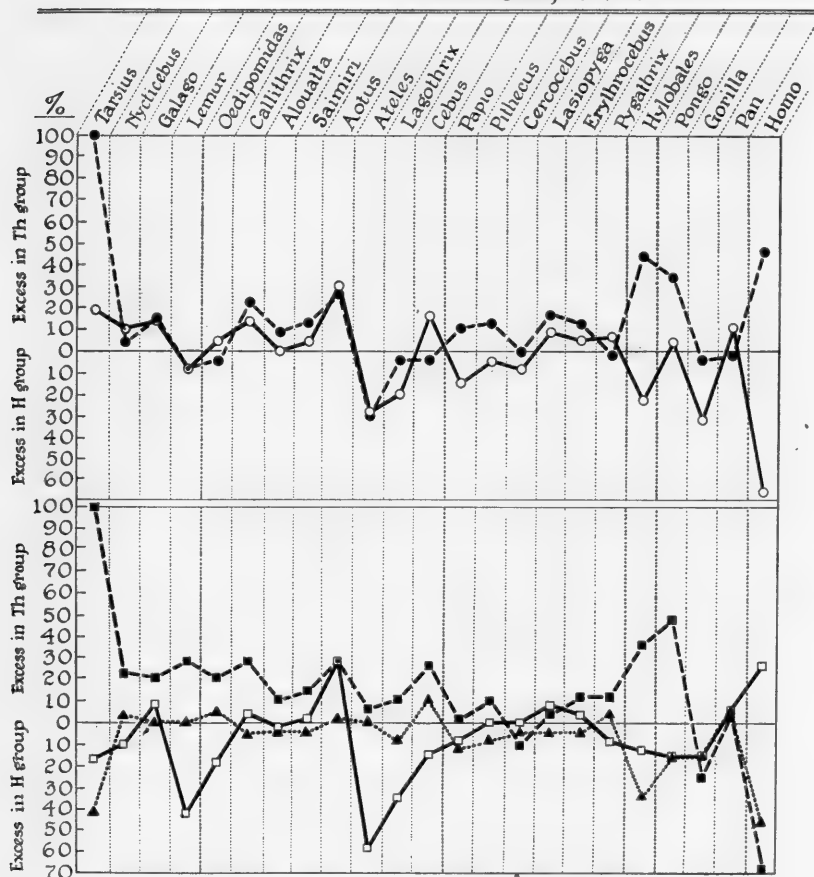
Perhaps the most striking finding in this comparison is the close parallelism between hand and foot existing in all the prosimians (except *Tarsius*, which as in many other dermatoglyphic comparisons has been shown to be an erratic member of its group) and in New World monkeys; lesser similarity between hand and foot is presented in Old World monkeys, and there is a sharp increase of unlikeness in gibbon, great apes and man.

The values for relative intensities of the thenar and hypothenar groups may be reduced to average values for all non-human primates. Though it is impossible at the present time to disclose the factors responsible for intergeneric variations in the intensities of the two groups, it is of importance to note that the collective trend revealed in the average is equality of these groups. The adjusted total intensity of the palms in the 22 non-human genera averages 3.49 (interdigital III being omitted, as pointed out above). The average intensity of the palmar hypothenar group is 1.74 and that of the thenar group, 1.75. Figure 600 shows in contrast that the tendency in the sole is toward higher pattern intensity in the thenar group. The average intensities of the plantar hypothenar and thenar groups in the 22 non-human genera are 1.52 and 1.29 respectively. In the human palm there is a marked departure from the average trend, the intensity of the hypothenar group being .69 and that of the thenar group

.14. The human sole presents an accentuation of the average trend, with intensities of 1.20 and .71 in the thenar and hypothenar groups respectively.

Our attempts to associate differential trends of hand and foot with unlike modes of locomotion and prehension appear to

Figure 600  
Comparisons in Palm and in Sole of  
Relative Intensity Values ~  
Based on Summation of Absolute Intensities of Th group (Th, I, II)  
and H group (H<sup>P</sup>, H<sup>S</sup>, IV).



Differences between Relative Intensities of Th and H groups:  
○—○ Th and H groups of Palm    ●—● Th and H groups of Sole  
□—□ Th group of Palm and H group of Sole  
■—■ Th group of Sole and H group of Palm  
▲—▲ Th group of Palm (above O line) and Th group of Sole (below O line)

have yielded little result. For example, in the three pronounced brachiators, *Ateles*, *Hylobates* and *Pongo*, there is agreement in possession of greater intensity in the hypothenar group of the palm than in the thenar, yet some non-brachiating forms display a like tendency though of lesser degree, and, to render the problem still more perplexing, comparisons of the foot are even less consistent. It is quite possible, of course, that an approach to this question on the basis of exacting analysis of varying methods of grasping and progression would reveal correlations which we have failed to find.

The next appropriate comparison involves the corresponding groups of palm and sole, the thenar group of the palm to be compared with the thenar group of the sole, and the hypothenar groups of the two members to be treated in the same manner. Since we are dealing with relative intensities, a representation of the thenar comparisons, as shown in figure 600, forms a mirror image of the relative intensities of the hypothenar group, which is therefore omitted to gain simplicity of the graph. The graph represents differences in relative intensity, hence zero differences and differences so small as to be negligible indicate likeness in intensity of the corresponding groups of hand and foot. In this as in other comparisons of pattern intensity the prosimian genera are found to be widely variable. The most marked unlikenesses between corresponding groups in palm and sole occur in *Tarsius*, *Hylobates* and *Homo*. This is taken to indicate that significant differences between corresponding groups of palm and sole occur in at least these three genera.

To supplement the foregoing comparisons of the thenar and hypothenar groups in the same member and of corresponding groups in palm and sole, comparisons are next drawn with the purpose of determining relationships between the thenar group of the palm and the hypothenar group of the sole and the converse relationship between palmar hypothenar and plantar thenar groups.

The differences in relative intensities are plotted in figure 600, where it will be noted that these two cross comparisons

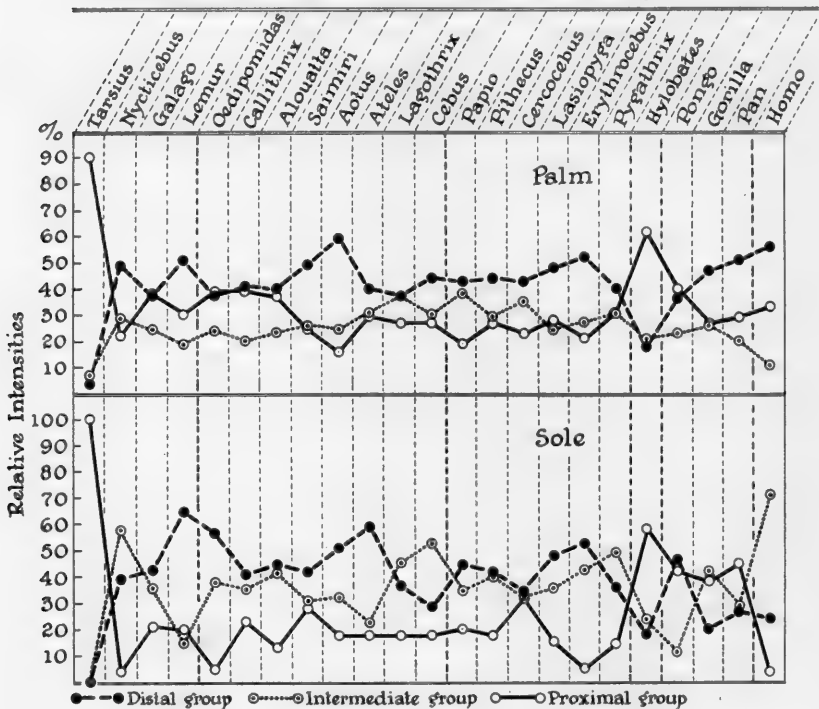
coincide or nearly coincide in Old World monkeys, some New World genera, in gorilla and in chimpanzee. Such coincidence evidences that in these forms there is little or no distinction between palm and sole when areas on reverse sides of the anatomical axis are compared. It would suggest negligible differential specialization of hand and foot insofar as that specialization may be expressed in pattern intensities. In contrast, extreme differences in these cross comparisons occur in *Tarsius*, *Lemur*, in several New World monkeys (especially *Ateles*, *Lagothrix*, *Cebus*), in *Hylobates*, *Pongo* and *Homo*. The finding naturally suggests unlikeness in regional functional specialization of palm and sole.

The comparisons combined in figure 600 may now be viewed collectively. It will be apparent that coincidence or close approximation of the results of all the foregoing comparisons may be interpreted as a sign of lack of differential specialization, applying to the two groups within the same member, to corresponding groups of the two members, and to the opposite groups in the two members. It may be inferred, therefore, that Old World monkeys and some New World monkeys as well as *Gorilla* and *Pan* show a generalization of pattern intensity in hand and foot. The extremes of distinction between palm and sole are noted in *Ateles*, *Hylobates*, *Pongo* and man. Inspection of the figure will show that while these four forms share the common trait of unlikeness between hand and foot, the regional and membral differences are inconsistent among them.

The components of the thenar and hypothenar groups, in disto-proximal succession, are next considered. The distal, intermediate and proximal units of the two groups are respectively combined to form new divisions for the examination of the relative intensities in regions which are separated transversely. The groups are: II and IV, I and  $H^d$ , Th and  $H^p$ . Inasmuch as our concern is with the relative intensities of these groups, their pattern intensities are reduced to percentile values, the percentages being based upon the total

Fig. 601

Comparisons in Palm and Sole of Relative Intensity Values  
Based on Summation of Absolute Intensities of the Distal (*II, IV*),  
Intermediate (*I, H<sup>d</sup>*), and Proximal (*Th, H<sup>p</sup>*) Groups



intensities of the six configurational areas involved. The results are shown graphically in figure 601.

*Palm.* In both Old World and New World monkeys, with the exception of Callithrichidae and Alouatta, there is a nearly constant relationship existing in all genera with regard to the relative intensities of the three groups. The distal group invariably has the highest intensity. The intermediate group is next in order, except in Lasiopyga (where the disparity is negligible), and the proximal group is further reduced in intensity (though equal to the intermediate group in Pygathrix). The described succession of relative pattern in-

tensities of these three groups in most monkeys is therefore a regular disto-proximal gradient. The prosimians, some New World monkeys, great apes and man conform in general to Old World monkeys only in that the distal group is characteristically the one which shows the highest relative intensity. Tarsius and Hylobates are the most conspicuous exceptions, in having the proximal group much elevated in pattern intensity and the distal group much reduced. In the prosimians, except Tarsius, in Callithrichidae, Alouatta, great apes and man the tendency is for the intermediate group to present the lowest intensity and the proximal group to occupy a middle place.

*Sole.* The relative intensities of the three groups in most genera conform to the disto-proximal gradient mentioned as characteristic of the palms of most monkeys. The prosimian genera are irregular with respect to this gradient. The only monkeys presenting departures are Lagothrix, Cebus and Pygathrix. In gibbon the great apes and man the seriation of pattern intensities of the three groups is widely variable. In Hylobates, exactly reproducing the condition in the palm, it is the proximal group which has the highest intensity and the distal group the lowest; this relative order occurs also in Pan, and is closely approached in Gorilla. The order in Pongo adheres to the general primate trend only insofar as it is the distal group which has the maximum intensity; the intermediate group has by far the lowest intensity. The singular position of man, where the intermediate group stands so far above the other groups in pattern intensity, calls for reference to the topographic distinctiveness of the hallucal pattern and its possible lack of complete homology with the first interdigital patterns in other primates with which it is compared. The hallucal pattern in man lies in transverse line with the interdigital series and simulates them also with respect to high pattern intensity. If this special feature be discounted, the group intensities in man would compare much more closely to those in Gorilla and Pan. It may be suggested that the more common sequence, in which the distal, intermediate and

proximal groups are progressively lowered in relative intensity represents the least modified regional relationship. While this sequence is itself somewhat modified, with reference to a theoretically more primitive condition in which all groups would be equal, it appears to be the strongest claimant for recognition as the simplest available basic order. Significant disorganization of that order may be taken to indicate profound regional specialization. Quite apart from any question which might arise as to our setting up the regular disto-proximal order as a standard of reference, it will be obvious that reversals such as are to be seen in *Hylobates* are acceptable evidences of regional specializations which differ from that standard. In the instance of *Hylobates*, it might be proposed that the extreme reduction of pattern intensity in the distal series is linked in some way with brachiation, notwithstanding that *Ateles*, though also a brachiator, adheres to the regular gradient of intensity in these three groups. The conditions in *Pongo*, another brachiator, resemble those described in *Hylobates*, and it may be added that the distinctiveness of the sole in *Hylobates* is approached by the sole of *Pan*. To single out the generic departures from the simple gradient order is thus not very fruitful if an attempt be made to correlate them with specific locomotor habits, however convincing it may be that these departures do indicate specializations.

#### RELATIONSHIPS TO THE ANATOMICAL AXIS

Of special interest in a consideration of regional variations of pattern intensity is the relationship to the anatomical axis of hand and foot. Interdigitals II, III and IV are best adapted to this comparison. In figure 599D it will be noted that in non-human primates the average values of these areas are such that in both hand and foot interdigital III presents a lower value than either II or IV. Inspection of the values for individual genera (tables 4 and 5) will show that with few exceptions they conform to the average. The exceptions of particular interest occur in the soles of *Lemur*, *Saimiri*,



Lagothrix, Cebus and Gorilla, where the sequence of values in the three areas under consideration is like that of the human *hand*:  $IV > III > II$ .

Another trend of departure from the average is to be found in the soles of certain Lasiopyginae (Papio, Cercocebus, Lasiopyga), where as in the human sole the maximum intensity is in interdigital III.

The sequential relations of interdigital intensity values in man indicate that the interdigital areas of corresponding name are not serially homologous in hand and foot with regard to the expression of pattern intensity. This finding is hardly unexpected, since in the human foot the anatomical axis is shifted from the characteristic orientation. According to Howell and Straus ('33):

"The four dorsal muscles [interossei] are primitively oriented with reference to an axis through the third toe. This is the condition in all monkeys and in some prosimians, but in others of the latter group the axis has shifted to the fourth digit. The axis passes primitively through the third toe in most gibbons, chimpanzees and orang-utans, but in occasional specimens of all three forms it has shifted medially to the second toe, the latter condition being normal for both man and gorilla."

The observations in non-human primates indicate that there is something inherent in the relationships of the anatomical axis which leads most commonly to a depression of pattern intensity in the configurational field which lies in that axis, usually interdigital III in conformity to the description quoted above. On this basis it might be expected that the human hand would conform to the trend evidenced in other primates, and that the human foot would present a shifting of the minimum intensity to interdigital II, thus conforming to the relations of other anatomical features. The observed values, however, suggest that some factor additional to axial relationships may influence pattern intensity. As shown in figure 599C, the minimum intensities are those of the palmar interdigital II and plantar interdigital IV. The reversed topo-

graphic relations of these areas are difficult to reconcile with any mechanism such as that which is assumed to be responsible for the usual axial reduction in pattern intensity in non-human forms. If these two areas be set aside as localizations of minimal intensity which are not influenced by relationships with the axis, then the two remaining interdigital areas are significantly aligned in reference to the anatomical axis. In the palm and sole alike the area having the lesser value, interdigital III in the palm or II in the sole, lies in the axis. We regard this relationship of pattern intensity to the anatomical axis as of the same fundamental meaning as other expressions of structure and variation centering about it. The differences of these expressions in the hand and foot of man include such diverse manifestations as digital lengths, localization of syndactyly, distribution of hair on the digits and distribution of dermatoglyphic patterns on fingers and toes.

Except in some prosimians, in which the longest digit of the hand is the fourth, digit III is the longest in primates (Schultz, '26; Midlo, '34). As for the toes of primates, the third is the longest as a rule. In some prosimians and New World monkeys the fourth toe may equal the third or even exceed it in length, while in man the longest toe is the second or the first (Schultz, '26). It will be evident that in primates generally the hand and foot present the longest digit in relation to the anatomical axis. Since in most forms this axis is in line with digit III in both hand and foot, the shifting tibialward of maximal toe length in man is of special interest in showing that there may be some significant association between maximal digital length and the axis. That such is the case is suggested by the relationship to the axis of other features. Before considering these, further attention should be given the principle of serial comparison which is illustrated in figure 599. In a typical primate, as just pointed out, maximal digital lengths occur in numerically corresponding digits of hand and foot. A graphic alignment of the human digits in serial order (fig. 599A), adjusted so that digits of greatest length coincide, leaves isolated the thumb and little toe, which

agree in hand and foot in being the digits of least distal reach. It is not impossible that this likeness of two marginal digits has morphological significance inasmuch as a similar relationship reappears in comparisons involving hair distribution on middle segments of digits and pattern intensity in interdigital areas.

Danforth ('21) has presented observations concerning the digital distribution of hair. He points out that the basal segments commonly present hair and that the terminal segments are invariably devoid of hair, while the middle segments vary with respect to its presence and amount. Only four digits, of course, are available for the full comparison. The maximum hair-bearing is on digit IV of the hand and digit III of the foot (fig. 599B). Comparison of the hand and foot not only shows that these two digits correspond as sites of maximum hair representation but it demonstrates also an almost exact agreement in three other couplets of digits: III and II of the hand and foot, respectively, IV and III of hand and foot, and V and IV. Perhaps as significant as this is the agreement of the index finger and little toe in their nearly complete suppression of hair. The relationship may be likened to that of digital lengths, where digit I of the hand and digit V of the foot, the marginal elements in the seriation, show minimal values. On the basis of these observations on hair, as well as the muscular relations which alone often are thought of in connection with the anatomical axis, and the more frequent occurrence of syndactyly in digits III and IV of the human hand and digits II and III of the foot, Danforth properly concludes "that the individual fingers and the individual toes are not serially homologous". M. T. Newman ('36) has drawn attention to a like finding in the apical patterns of fingers and toes in man. He points out that pattern distributions on individual fingers and toes indicate "that if the foot is to be compared with the hand, the foot as a whole must be shifted one digit tibialward". Thus, for example, tibial loops (equivalent to radial loops of the hand) have their maximum frequency on the great toe (M. T. Newman;

Takeya, '33), one digit removed from the place in the digital sequence of the index finger, which presents the maximum concentration of radial loops. While no studies of the correlation have been made in the same sample, it is significant that statistics on the frequencies of finger-print types indicate that digits IV of the hand and III of the foot, the centers of maximal representation of hair, are also the sites of greatest frequency of whorls. We have translated Newman's records of the percentile frequencies of pattern types into pattern intensities (fig. 599A). The result shows a nearly exact agreement of digits II through V in the hand with I through IV in the foot. The thumb and little toe can not be partnered as was done in other comparisons of digits, since they represent respective elevation and depression of pattern intensity.

It is emphasized above that in both palm and sole the characteristic site of minimum pattern intensity in the interdigital areas of non-human primates is interdigital III, the configurational field which lies in the anatomical axis in both members. In man the unlike axes of hand and foot are associated with unlike foci of lessened pattern intensity. Interdigital II in the palm and IV in the sole possess the actual minimal intensities of these members, recalling the comparable relations of digital length and hair occurrence in marginal digits. The findings suggest that factors other than axial position may lessen pattern intensity. Considering the remaining two areas in each member, III and IV in the hand and II and III in the foot, the principle previously stated in reference to non-human primates still holds; of these two areas in the foot the lesser intensity is that of interdigital II, which is in the anatomical axis, and in the hand it is likewise the area in the axis, here interdigital III.

Again in man there occur at the distal plantar margin and at the distal palmar margin variations which are differently localized in foot and hand. To appreciate these variations, there should be noted (figs. 587-593) the characteristic digital triradii, seated just proximal to the bases of digits II-V. In the sole there is a tendency, most frequently expressed in rela-

tion to digits II and III, to approximation and suppression of these digital triradii. This tendency is an abortive expression of syndactyly (Cummins and Sicomo, '23; Ford, Brown and McCreary, '41, p. 52). The comparable manifestation in the palm is less frequent, but when it occurs the involvement is usually related to digits III and IV; even in the absence of such marked approximation or obliteration of digital triradii, measurements have shown that the tendency is nevertheless present (Cummins, Leche and McClure).

In the absence of measurements of ridge breadth on the toe tips and sole it is impossible to draw comparisons of variations in ridge breadth with respect to the anatomical axes of the two members; yet the observations of ridge breadth in the hand (Cummins, Waits, and McQuitty) yield suggestive indications of regional variations at least partially under apparent regulation by factors associated with the anatomical axis. On the finger tips, for example, ridges are finer ulnarwards from the axis than they are in the digits radialwards from it. In the distal palm the finest ridges are in the anatomical axis. It is to be hoped that similar measurements of the sole may be made available for comparison.

#### BILATERAL ASYMMETRY

The occurrence in man of unlike pattern frequencies in right and left hands is recognized. Studies in diverse racial populations have demonstrated in right hands, among other bimanually different trends: a higher frequency of whorls on the finger tips (Bonnievie, '24, and others); more abundant patterns in the hypothenar, second and third interdigital areas; and a lesser frequency of patterns in the thenar/first interdigital and fourth interdigital areas (Cummins, Leche and McClure; H. H. Newman, '30). There are indications that some of the trends of bimanual difference are altered in the left-handed (Keith; Bettman, '32; Leche, '33; H. H. Newman, '34; Cummins, '40; Rife, '41). Though the specific dermatoglyphic trends associated with functional dominance of one or the other hand are not yet fully established, the

existence of bimanual differences in the dermatoglyphics is in itself of interest as one of the expressions of unlikeness of the body halves. The only previous examination of asymmetry of pattern frequencies in a non-human primate, chimpanzee (Cummins and Spragg), has demonstrated bimanual differences which in part conform to those already known in man, a finding which gives added incentive to a broader survey of the question.

As to the foot, asymmetry has been emphasized in reference to patterns of human toes (M. T. Newman). On the toes of right and left members the pattern types display unlikenesses of frequency, but differing from those of the fingers with respect to localization on digits and side. Investigation of asymmetry of plantar features has been neglected, and while some authors (e.g., Hasebe, '18; Takeya, '34) have recorded separately the frequencies of configuration types in right and left soles, so slight have been the bilateral differences appearing in collections of material assembled for racial comparison that many reports have been published with the frequencies of right and left sides combined. This situation has led us to re-examine the original tally sheets of plantar configurations in some of our racial collections for the needed separate summaries of pattern frequencies in right and left soles, the results being converted to pattern intensity values. The findings indicate the existence of subtle bipedal differences, which are here presented for comparison with other primates (table 6).

*Regional asymmetries.* The separate listings of pattern intensities in the several regions of palm and sole are included in tables 7 and 8 for those genera in which reasonably adequate numbers are available. For more ready analysis of bilateral differences, and as a measure to offset the limitations of small numbers in some genera, the following groupings have been made for comparison: New World monkeys, gibbon, great apes, and man. In the three groups which combine several genera each, the figures of tables 7 and 8 are pooled in weighted averages. Both weighted averages and direct averages have

been calculated within these three groups. In this one application, involving individual configurational fields, the weighted averages were thought to be preferable since the direct averages give undue value to the genera represented by smaller numbers. The disadvantage of discounting possible distinctions of some genera seems to be of lesser importance than the shortcomings of the direct average. Figure 602 presents a condensation of these findings. To emphasize the topography of fields showing right or left ascendancy of pattern intensity, broken lines are inserted as boundaries of such fields. It is noteworthy that these territories seem to resolve naturally, requiring no irregularities of zonation. As in other comparisons, sight must not be lost of the fact that we are dealing with quantitative determinations of highly variable traits in series which are too small to yield absolutely dependable values.

Because of familiarity with human bimanual differences, it may be well to begin the discussion with the distinctions between right and left palms in man. In this instance there is assurance of stability of such differences inasmuch as they have been repeatedly shown in large collections of material. As pointed out by Cummins, Leche and McClure, ascendancy of patterns (higher percentile frequencies) in left hands occupies a diagonal field embracing Th, I and IV, thus isolating the two regions in which patterns are more frequent in right hands. Conversion of the determinations to pattern intensity values yields the same distribution, shown in figure 602. No one of the non-human primate groups exactly parallels the conditions in the human palm, yet in the New World monkeys the only significant departure is the ascendancy on the right hand of interdigital IV. The great apes display a complete transposition of the conditions in Old World monkeys, the fields of right and left ascendancy being reversed in all regions, if the bilateral equality of  $H^p$  of Old World monkeys be regarded as a partial obliteration of right ascendancy. Compared to New World monkeys, great apes differ only in that the field of left ascendancy is shifted distally to involve

interdigital I and II instead of Th and I; with this shift there is of course a reversal to right ascendancy of Th in this group. The gibbon presents no single region with left superiority.

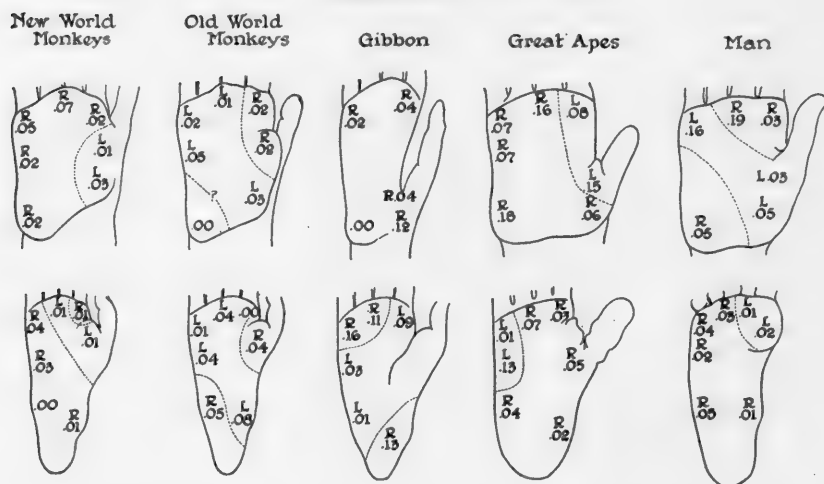
Figure 602  
Regional Bilateral Differences  
in Pattern Intensity ~

R... excess in right member.

L... excess in left member.

O... no bilateral difference, though patterns are present.

Symbols...are not entered in regions lacking patterns.



In considering the sole, again man may be mentioned first. The small magnitude of bilateral difference, as well as the inconsistency of the direction of difference in various samples (table 6), indicate a lesser degree of asymmetry than that of the palm. They indicate, too, the need of great caution in interpreting the differences observed in the smaller collections of non-human primates. In the combined material, left superiority is confined to Th<sup>d</sup>/I and II. The excess of pattern intensity in Th<sup>d</sup>/I of left soles is undoubtedly significant, since the discrepancy is repeatedly expressed in all but two of the twelve racial samples. The left superiority of interdigital II is less consistent among the samples. Reversal to right superiority in "mongoloids" (Eskimos; three series of North



American Indians; a collection of Spanish-Americans in which other signs of Indian admixture have been noted — Cummins, '41) and equality in a series of Maya may point to the existence of racial differences in bipedal asymmetry. This is

Table 6

Bipedal Comparisons of Pattern Intensity and Pattern Frequencies in Man -

Series	Number of Individuals	Th <sup>d</sup> /I		II		III		IV	
		R	L	R	L	R	L	R	L
European-American <sup>1</sup>	200	.83	.86	.20	.26	.62	.56	.21	.14
European-American <sup>2</sup>	100	.82	.82	.22	.23	.64	.59	.16	.16
European-American <sup>3</sup>	100	.84	.85	.24	.25	.64	.60	.14	.06
Jews <sup>4</sup>	100	.82	.85	.38	.38	.78	.75	.21	.15
Spanish-American <sup>5</sup>	96	.75	.77	.23	.30	.58	.52	.08	.07
Spanish-American <sup>6</sup>	110	.81	.83	.24	.23	.65	.57	.08	.05
Hopi <sup>7</sup>	59	.67	.72	.37	.30	.39	.44	.03	.06
Navajo <sup>8</sup>	95	.78	.83	.19	.15	.53	.50	.06	.06
Pueblo <sup>9</sup>	131	.74	.76	.17	.12	.50	.48	.11	.12
Maya <sup>10</sup>	124	.78	.76	.19	.19	.52	.50	.16	.10
Eskimo <sup>11</sup>	31	.57	.63	.24	.21	.44	.55	.05	.00
Negro <sup>12</sup>	98	.87	.88	.25	.28	.58	.63	.30	.26
Weighted average of 12 groups	1244	.79	.81	.23	.24	.59	.56	.15	.11
Percentile frequencies of all patterns & vestiges.	1244	.93	.94	.26	.29	.71	.68	.18	.14

<sup>1</sup> Wilder '22, <sup>2,3</sup> Cummins and Midlo '26, <sup>4</sup> Cummins and Midlo '27,  
<sup>5</sup> Cummins '41 (Bernalillo), <sup>6</sup> Cummins '41 (Chamita), <sup>7,8,9</sup> Cummins '41,  
<sup>10</sup> Cummins and Steggerda '36, <sup>11</sup> Cummins '35, <sup>12</sup> Cummins '30.

all the more strongly indicated in the light of the findings of Takeya in a collection of 1000 Chinese, where interdigital II is again ascendant on right soles, though the other three plantar areas agree in the direction of asymmetry with the human averages shown in table 6.

The human sole, like the palm, compares most closely with the sole of New World monkeys (fig. 602), where the discrepancy involving plantar interdigitals II and III is probably insignificant, indicating that there is no real difference in the bilateral plantar asymmetries of man and New World monkeys. Both man and New World monkeys exhibit a zone of left superiority confined to a limited disto-tibial region. A curious reversal of this condition occurs in the great apes, where there is a similarly limited region of left superiority lying in the disto-fibular zone and involving H<sup>d</sup> and interdigital

Table 7  
Bimanual Comparisons in Pattern Intensity

Genus	No. of Palms*		Hd		H <sup>P</sup>		Th		I		II		III		IV	
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
<i>Alouatta</i>	8	10	.22	.08	.96	.98	.50	.68	.85	.82	.70	.72	.73	.62	.100	.100
<i>Saimiri</i>	9	10	.02	.07	.87	.85	.07	.11	.91	.96	.93	.95	.87	.87	.96	.91
<i>Ateles</i>	19-20	22-26	.65	.66	.85	.83	.19	.16	.37	.44	.66	.65	.06	.00	.73	.66
<i>Cebus</i>	18-19	17-19	.06	.00	.94	.92	.02	.00	1.00	1.00	1.00	1.00	1.00	1.00	.57	.46
<i>Papio</i>	10-14	11-14	.76	.85	.90	.87	.00	.00	1.00	.94	1.00	1.00	.95	.95	.97	1.00
<i>Pithecius</i>	45-46	40-43	.43	.44	.92	.92	.29	.33	.90	.85	.97	.96	.96	.98	.99	1.00
<i>Lasiopyga</i>	8	8	.00	.00	.90	.93	.15	.35	1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
<i>Erythrix</i>	7	7	.23	.49	.77	.80	.43	.43	.83	.97	.91	.77	.80	.80	.80	.89
<i>Hylobates</i>	22	22	.00	.00	.84	.84	.24	.12	.37	.33	.04	.00	.00	.00	.02	.00
<i>Pongo</i>	8-9	9-10	.00	.00	.95	.98	.27	.16	.76	.62	.73	.50	.13	.08	.44	.44
<i>Gorilla</i>	6	4-5	.50	.16	.37	.64	.13	.00	.13	.28	.17	.85	.87	.80	.47	.64
<i>Pan</i>	37-40	39-40	.06	.02	.46	.15	.27	.22	.21	.45	.41	.49	.29	.10	.56	.45
<i>Homo</i>	374	374	.00	.00	.30	.25	.03	.08	.01	.04	.06	.03	.48	.29	.33	.49

\* Double entries indicate variable numbers available for the determinations of the several regions

IV. The soles in Old World monkeys and in gibbon present diagonal fields of left superiority separating two zones of right superiority, but in these groups the regions involved are essentially reversed.

Comparison of regional asymmetries of palm and sole in the same group or genus discloses resemblances and differences which are suggestive of varying intermembral specializations. The zones of right and left superiority are in virtual agreement in palm and sole only in Old World monkeys, the group containing the pronounced walkers. Next in order of inter-

membral difference, New World monkeys present unlike zonations in palm and sole, but the differences are small. The contrasts between hand and foot in gibbon, in great apes and in man are marked, and among them the intermembral differences vary in regional distribution. Habits of prehension and locomotion, including brachiation, distinguish these forms from Old World monkeys, in which we have pointed out likeness of hand and foot. The factors accountable for the differing intermembral conditions in gibbon, great apes and man

Table 8  
Bipedal Comparisons in Pattern Intensity

Genus	No. of Soles*		H <sup>d</sup>		H <sup>p</sup>		Th <sup>p</sup>		I		II		III		IV	
	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L
Alouatta	12	10	.58	.80	.13	.08	.38	.40	.85	.94	.73	.80	.58	.54	.97	.96
Saimiri	9-10	11	.40	.11	.32	.53	.46	.58	.84	.80	.62	.49	.60	.56	.86	.73
Ateles	18-19	15	.37	.33	.04	.05	.31	.20	.01	.11	.29	.29	.15	.05	.69	.75
Cebus	19-20	16	.39	.39	.25	.09	.27	.21	.91	.75	.08	.01	.31	.43	.68	.56
Papio	11-13	11-13	.48	.60	.60	.30	.40	.45	.97	.91	.95	.93	.98	.97	.97	.94
Pithecius	46-49	41	.77	.78	.10	.06	.57	.69	.91	.87	.78	.80	.70	.68	.93	.92
Lasiopyga	8	8	.35	.50	.30	.00	.30	.40	.90	.93	.90	.90	1.00	1.00	1.00	.98
Pygathrix	8	6	.95	1.00	.00	.00	.43	.30	.85	.73	.55	.40	.15	.47	.53	.70
Hylobates	22	20-21	.01	.04	.11	.12	.62	.49	.00	.00	.07	.16	.11	.00	.16	.00
Pongo	11	9	.07	.09	.07	.00	.58	.69	.11	.09	.40	.27	.20	.13	.36	.47
Gorilla	8	7	.40	.63	.10	.46	.73	.54	.50	.29	.10	.00	.48	.34	.40	.34
Pan	32-33	32	.30	.44	.29	.18	.64	.61	.18	.17	.13	.15	.11	.05	.39	.38
Homo	**		.47	.45	.10	.07	.10	.09	.79	.81	.23	.24	.59	.56	.15	.11

\* Double entries indicate variable numbers available for the determinations of the several regions.

\*\* The data for I, II, III, and IV are based on 1244 individuals, for H<sup>d</sup> and H<sup>p</sup>, 200, and for Th<sup>p</sup>, 50.

must remain for the present unknown, though it is likely that there is at least a partial functional explanation for the differences, on the same principle which is suggested as the source of their distinction collectively from Old World monkeys.

It is not intended to suggest that the explanation of the differences between hand and foot in regional asymmetries is concerned only with functional influences. That other factors are introduced is evidenced, for example, by the similarity of

the hand of the great ape and the human foot, where the functional agreement would be negligible. In further illustration it may be pointed out that the human palm resembles the soles of Old World monkeys and gibbon in the general principle of possessing a diagonal field of left ascendancy separating two zones of right superiority, a principle which is at least potentially present also in the hand of Old World monkeys. The complexity of the developmental substrate which leads to bilateral differences in pattern intensity may be best appreciated by considering the status of bimanual differences in man. It must be remembered that the distinctions of right and left hands are expressed only in trends, and that many individuals lack expressions of such trends. Studies of right- and left-handed individuals indicate that the prospective functional dominance of one or the other hand plays some part in regulating the dermatoglyphic expression in the individual. The occurrence of racial differences in bilateral asymmetry (see suggestion above in connection with bipedal differences, also Poll, '38, on an expression of asymmetry in finger-tip patterns) renders the situation all the more complicated. In the other primates, as well, there may exist phenomena of similar complexity. It would be hazardous to place undue emphasis on bimanual and bipedal regional differences in view of the small numbers on which the statistics are based.

*Aggregate asymmetries.* Having dealt with regional asymmetries in pattern intensity, a consideration of asymmetries in which the whole members are variously compared may next be introduced. Several measures of bilateral asymmetry, based upon data in tables 7 and 8, are supplied in table 9 and discussed below: index of asymmetry; membral asymmetry; total asymmetry; relative asymmetry of the palm. It will be evident that cancellation effects may be introduced when regional asymmetries are pooled.

For arriving at the *index of asymmetry* of a genus the total intensities of right and left palms or soles are expressed in a proportion between right and left sides:  $100 \times$  (the larger of the two total intensities whether right or left, divided by

the smaller); when the greater intensity occurs on the right side this result is final, but if on the left side, the excess of the result over 100 is subtracted from 100. Indices larger than 100 accordingly indicate greater intensity on the right side, while figures less than 100 show that the higher intensity is on the left; in either case the magnitude of bilateral difference is reflected in the value of the index.

*Membral asymmetry*, like the following measures of asymmetry, are stated in percentages of total intensities. The percentage statement is followed as an adjustment to the widely different total intensities among genera. In table 9

Table 9  
Aggregate Asymmetries in Pattern Intensity  
(See text for explanation)

	Index of asymmetry		Total asymmetry per cent	Relative asymmetry of palm	Membral asymmetries per cent			
	Palm	Sole			Palm		Sole	
					Right	Left	Right	Left
Alouatta	101	93	10.8	0.9	5.6	4.5	2.4	8.8
Saimiri	102	108	14.7	0.2	1.5	3.4	15.4	8.7
Ateles	103	104	15.4	0.3	5.4	2.4	13.4	9.6
Cebus	105	118	15.2	0.2	4.6	0.0	19.7	4.9
Papio	99	105	7.7	0.3	1.6	2.1	7.9	3.3
Pithecus	99	99	4.0	0.5	1.0	1.6	2.3	3.1
Lasiopyga	95	101	8.5	0.4	0.0	4.4	6.7	5.9
Pygathrix	92	96	19.6	0.5	2.9	10.1	11.6	15.0
Hylobates	117	133	34.9	0.3	14.6	0.0	37.0	16.0
Pongo	118	103	24.3	0.6	16.2	1.1	16.2	13.8
Gorilla	72	104	55.9	1.2	20.5	37.7	25.8	22.7
Pan	120	103	34.2	2.5	31.0	17.0	10.8	8.1
Homo	103	104	25.5	6.5	22.3	20.3	5.3	1.3

the membral asymmetries, calculated as described below, are listed for right and left sides for both palm and sole. For each of the configurational fields the pattern intensities of right and left sides were compared. The differences between right and left sides are set down as asymmetries, allotted to the side bearing the excess. Totalled, the excess is calculated as the percentage of the total intensity of that side.

*Total asymmetry* refers to collective asymmetry, irrespective of distribution on palm and sole and on right and left sides. The figure is obtained by adding all the absolute differences in pattern intensity of all members, then converting

it to the percentage of the combined total intensities of palm and sole.

*Relative asymmetry of the palm* is the relationship of total bimanual asymmetry to total bipedal asymmetry (obtained from the membral asymmetries listed in table 9). The sum of the right and left asymmetries of the palm is divided by the corresponding sum of the sole, the result being expressed as a proportion. Unity would indicate equality of asymmetries of the hand and foot.

The least *total asymmetry* occurs in the Old World monkeys, though in this group *Pygathrix* represents an exceptionally high asymmetry which is comparable to that of New World monkeys. In the higher primates asymmetry is greater than in monkeys: monkeys < Pongo = Homo < Pan = *Hylobates* < Gorilla. These statements are based upon the percentage of total asymmetry rather than with the use of the index of asymmetry. The index is of less significance for such comparison, embodying the total intensities of right and left palms and soles without regard to directions and amount of asymmetry of individual regions. In spite of cancellation effects which are inherent in the index, Old World monkeys retain their position as the least asymmetrical forms, with *Pygathrix* again as an exception. The New World monkeys and man are next in order of increasing asymmetry, but *Cebus* presents a higher asymmetry which equals that of the great apes. *Hylobates* exhibits the maximum asymmetry on the basis of the index.

The *relative asymmetry of the palm* is of particular interest. In monkeys palmar asymmetry does not even approach the magnitude of asymmetry of the sole, with the single exception of *Alouatta*. The higher primates form a noteworthy sequence of increasing relative asymmetry. In *Hylobates* asymmetry of the palm is just about one third that of the sole; Pongo, Gorilla, Pan and Homo are ranged in a regular progression of increasing relative asymmetry of the palm (the figures approximating an orderly increase through the higher pri-

mates, so that if *Hylobates* were rated as 1, *Pongo* would be 2, *Gorilla* 4, *Pan* 8, and *Homo* 22).

With regard to the amount of asymmetry in the right and left members, the prevailing relation in the sole is for intensities to be greater on the right side, but in the palm right and left sides are about equally divided among the genera as to direction of ascendancy in pattern intensity. It is possible that special significance should be attached to the greater pattern intensity of left palms in the Old World monkeys, where this disparity is consistent through all four genera; *Saimiri* and *Gorilla* are the only other genera presenting the inferior pattern intensity in right palms.

The occurrence of marked differences among the groups of primates in the magnitudes of bilateral asymmetries of pattern intensity recalls the findings recorded by Schultz ('30) in the lengths of bones of right and left sides. He finds that bilateral symmetry is more prevalent in the lower primates than in the higher groups, and to this extent the results agree with those obtained in the comparisons of pattern intensity. Within the higher primates the seriations of progressive increase in asymmetry of bone lengths and pattern intensities are quite different, in fact showing in some respects a tendency toward a reversal of order.

The possible interrelationship of asymmetries in pattern intensity and functional sidedness has not been investigated in any primate except man. With the appearance of the report by Finch ('41) on tests of handedness in thirty chimpanzees, it was at first hoped that material in the writers' collection might afford an opportunity to follow up this question. The animals used by Finch are in the colony of the Yale Laboratories of Primate Biology, the same source as the material studied by Cummins and Spragg in a survey of dermatoglyphics of *Pan*. Through lack of coincidence of individuals recorded for handedness and represented by prints, the number available for correlating handedness and dermatoglyphic traits is so reduced that little can be gained; even the complete series of thirty animals would have been question-

ably adequate, and when that number is reduced to seventeen, as it is in the instance of comparisons in pattern intensity of finger tips, it is hardly surprising that evidence of correlation between pattern intensity and functional sidedness was not obtained.

## DISCUSSION

### THE CONDITIONING OF SPECIFIC CONFIGURATIONS

The basis of correlation between pads and dermatoglyphics has been variously interpreted. The divergent conclusions of different workers may be presented briefly.

One view is that supported by Whipple and by Wilder. Holding that the primary function of epidermal ridges is to prevent slipping in walking or in prehension, these writers claim that ridges are aligned at right angles to the force which tends to produce slipping (or to the resultant of such forces). Quoting from Whipple, "The shape of the pad elevation, the direction of flexion, and the direction of motion, are the factors determining the direction of the slipping force, and therefore the direction of ridges." It will be apparent that this interpretation implies the operation of Lamarckian factors, as does that of Kidd, who lays emphasis on the service of ridges and their pattern arrangements in rendering the tactile sense more acute. Schlaginhaufen, without committing himself to the evolutionary mechanism accounting for pattern formations, points out that patterns provide for more refined tactile discriminations than do open fields.

A third view, in contrast to interpretations which make functional utility the agency of determining the character of the ridge configurations, emphasizes developmental mechanics. This position is implicit in the statement of Hepburn that a pattern "has its character determined by the position, shape and dimensions of the particular eminence [on which it lies]". He does not elucidate how these factors would influence the pattern. Kollmann advanced the suggestion that ridge direction is determined by stresses incident to growth of the part.



Kolossof and Paukul ('06) analyzed ridge direction on a mathematical basis, pointing out that observed ridge directions are in keeping with the mechanical conditioning described by Kollmann.

Cummins and Sicomo, and Cummins ('26), resort to the observation of dermatoglyphics in developmental defects of human hands and feet as a substitute for experimental analysis of the factors which condition ridge direction. The material includes cases of syndactyly, polydactyly and other more grave involvements of form of the members. The cogent elements of the evidence and the main conclusions are:

“The causation of ridge direction, hence the source of aberrant configurations in the abnormal material, is suggested when from case to case it is found that the normal plan of configurations undergoes a marked modification or is even suppressed. It would appear that there are no predetermined limits to the potencies of ridge direction, actual expression of ridge direction being dependent in some manner upon factors which are causally related to the formation of contours.

Form (contour; relief) connotes differential growth, and the control of ridge alignment must be exercised by growth of the parts during the period of ridge differentiation.”

Bonnevie ('24), on the basis of the digital distribution and inheritance of finger-tip patterns as well as five cases of polydactyly, also concludes that there is probably a causal relationship between the form of the apical pads of the fetal digits and their ridge configurations. Further studies by Bonnevie ('27, '29, '31 and '32), Cummins ('29), Schaeuble ('33) and Abel ('35, '36 and '37) have extended the information on embryogenesis of dermatoglyphic patterns, but for the present purpose only the immediately relevant generalizations need be given.

In the human fetus the critical period of ridge differentiation is in the third and fourth months. Epidermal ridges are not formed simultaneously over the whole palmar and plantar surfaces, nor, according to work now in progress (Cummins), are the hand and foot synchronous in ridge de-

velopment. Prior to and at the time of ridge differentiation the previously more prominent volar pads are in process of involution. A pad which remains prominently elevated and more or less definitely circumscribed will determine, by virtue of its local complex of growth stresses, the formation of a definite pattern, its specific character varying in accord with the contour and circumscription of the pad.

Valleys in the volar reliefs, as instanced by the sunken parathenar area, like the pads elevated from the surface, represent foci of local irregularities in growth. Hence they are potentially seats of production of patterns or of regional irregularities in ridge direction.

A triradius is formed at the point of junction of three local growth complexes, its triangular composition indicating the action of forces from three directions. The topography of triradii on the palm and sole follows a fairly consistent plan. This plan is discussed by Whipple from the standpoint especially of the arrangement of triradii in reference to pads and to the skin folds which adjoin pads in many mammals. Schlaginhaufen constructs an elaborate scheme of the placement of triradii and he emphasizes their variations among the primates; Bychowska follows the same scheme in her analysis of the primate palm. From the view of developmental mechanics the basis of a morphologic plan of the triradii is obvious. The mutual conjunctions of eminences and their relations with the bases of digits and other marginal irregularities agree in a general way throughout the primate scale, inasmuch as there is a basic morphologic plan of the pads. Since, however, modifications of pads bring about correlated variations in their number and placement, the identities of individual triradii are sometimes not readily determined. Our decision to omit a consideration of these features in the present study was based upon the belief that the fundamentally important variations of dermatoglyphics are pattern expressions, and that the triradii are secondary elements, often present, absent, or displaced through fortuitous developmental

circumstances that have negligible significance in the desired comparisons.

It may be assumed, though no relevant comparative studies are available, that the same fundamental processes of development are concerned in the elaboration of dermatoglyphics in non-human primates. In some genera of prosimians and monkeys the volar pads attain a development far greater than that observed in man, persisting in the adult as prominent and bluntly pointed elevations, each more or less definitely circumscribed. It is in such forms that patterns are expressed more constantly than in the human palm and sole. On the basis of comparing fetal pads in man, macaque and *Tarsius*, it is evident that groups showing great unlikeness in adult pad expression and in dermatoglyphics are brought into closer relationship if observed in the period of maximum pad development. Such accentuation of similarities in fetal stages is in keeping with increasing resemblances of other features among different forms in progressively earlier development. Unlikenesses among the groups, with respect to dermatoglyphics, are the associates of unlikenesses in the form, subsidence, and circumscription of pads; differences in general form of the hand and foot also are correlated with different conditionings of ridge direction. It should be reemphasized that

“dermatoglyphic variations are so numerous and so manifold that they reveal many variables which though influenced by similarly variable pad reliefs are of a magnitude far exceeding that actually observed in the pads. It is impossible to reduce the pad variables to a reliable quantitative expression, and the character of the observed variables is such that they must be quite different in two compared pads to be detected at all.” (Cummins, '29.)

The fetal behavior of volar pads is to be taken both as a reflection of phylogenetic history and as an ontogenetic anticipation of definitive volar reliefs, which have a functional relationship with varying uses of the members. The differences in use of the anterior and posterior members in the same animal, together with the varying habits of different

primates, introduce factors of variation in the pads concerned. While it is hardly sufficient to characterize a primate as essentially a walking form or a brachiator, acquaintance with the precise manner of using the hand or foot is so limited that distinctions cannot be drawn except in general terms. Even such exacting observations on behavior as those of Bingham ('32) on the gorilla, of Carpenter ('34, '35, '40) on the howler, red spider monkey and gibbon, and of Nissen ('31) on chimpanzee have not disclosed a sufficient foundation for detailed correlations of uses of the members and modification of volar pads. It is suggestive, nonetheless, that some dermatoglyphic distinctions seem to point to an association between differential habits and the dermatoglyphics. The Old World monkeys, the primarily walking group of primates, are shown to possess high pattern intensity; the palm and sole present little difference in its expression, except in genera characterized by greater arboreal habit, *Pygathrix* especially, where the palm has much higher intensity than the sole. The pattern intensity is lower in New World monkeys, which are distinguished from those of the Old World by their generally more pronounced habits of grasping and climbing. The lowering of pattern intensity being more marked in the sole than in the palm, there is indication in this group of significant differential use of the members. It is also noteworthy in this connection that in the New World monkeys which display areas of incomplete ridge formation the sole presents a greater expanse of ridged skin; in the rare instances of incomplete ridge formation in Old World monkeys it is only the palm which is so characterized. The great apes and man provide further illustration of correlation between dermatoglyphics and differential use of the members. *Pongo*, a brachiator, shows a much higher pattern intensity in the palm than in the sole; that relationship is completely reversed in man, the only primate in which the hand is virtually excluded as a locomotor member. In *Pan*, a form in which on the basis of Nissen's observations it would be difficult to qualify either pair of members as dominant in locomotion, the palm and sole display equal pattern intensities.

## CRITERIA OF PRIMITIVENESS AND MODIFICATION

*The "primitive" configurational field.* The question of what constitutes the primitive state of an individual configurational field naturally arises in any comparative approach. Sequences of pattern types may be traced in continuous series from a well developed concentric whorl through steps of transition to a loop pattern, which in turn may be traced to complete loss of pattern character in the state of an open field. Such series of steps, it is obvious, are revealed not in the ontogeny of the single configuration but rather in a selected collection of patterns. One might read the scale of pattern development from either direction, were it not for the intimate associations of pads and patterns. The primitive pattern may be justly regarded, following Whipple and Wilder, as the type which is associated with that form of pad which has most primitive character. This reference to conditions of pads suggests that, of all configuration types, whorls might be rightly viewed as primitive (though, as noted just below and in the later discussion of the affinities of prosimians, this position can not be maintained without reservation). Whorls occur on pads which are prominently elevated as more or less pointed mounds. The occurrence of a whorl, however, is not necessarily dependent upon the presence of such a mound in the adult. The pads may persist in the fetus only long enough to condition whorl development, later subsiding into a relief which is not sensibly different from that of other slight elevations bearing configurations of quite different types. In some non-human primates which have pads that persist in what is essentially an approximation of the fetal condition (*Pithecus* and presumably all other forms which exhibit conspicuous pads in the adult), an actual correlation between the character of the pad reliefs and grades of pattern development is observable in the adult; but in other forms, as in man and great apes, "primitive" whorls and pattern types closely resembling them may occur in the absence of reliefs presenting primitive modelling. It is therefore the fetal pads which provide a key to interpretation, since the configurations are determined in their

definitive form and undergo no change even though the eminences are subsequently modified. We are, however, entitled to consider the most highly developed patterns as primitive in the sense that they express the maximum degree of fetalization of the pads which are responsible for their production. Whether the pads viewed as primitive are so actually is problematic. It is merely that these fetalized pads are of the form most widely present among mammals generally, and prevalence may not be a safe criterion of primitiveness. Furthermore, the extreme differences in dermatoglyphic expressions among some human races illustrate that categories of primitiveness in the dermatoglyphics of primates may be vitiated by the introduction of pattern-determining factors which are independent of those more directly related to a phylogenetic sequence.

The complications attending search for the primitive configuration are exemplified in the prosimians. The several genera within this one group include the total range of variation from the most "primitive" to the most highly specialized. *Galago*, for example (figs. 29-32), presents consistently in palm and sole whorls and whorl-like patterns. *Tarsius* (figs. 9-16), in contrast, shows almost a total suppression of patterns, while the other genera form transitions between these extremes. Likewise among both monkeys and apes, and even among human races, there are grades of variation from the more "primitive" to the "advanced" condition in which patterns are less well developed and less frequent; such variations are both intergeneric and intrageneric or intraspecific. From the observations assembled by Dankmeijer it is clear that the marsupials likewise run the gamut of dermatoglyphic expression, some forms being primitive in the sense of having abundant whorls, and others possessing only open fields, while some genera are even so primitive as to lack ridges.

Such attempts to trace dermatoglyphic patterns from an assumed primitive stem through steps of progressive advance lead to still other uncertainties. It seems to be quite clear that the presence of ridges is an advance over an epidermal

structure in which only rings and "warts" occur. Naturally there can be no whorl or any type of pattern at this level of epidermal specialization. Even in forms presenting actual ridge formation in areas of limited extent the potential expressions of patterns may be restricted by the lack of formed ridges. In the sole of *Aotus* (figs. 138-149), for example, the hypothenar region is only incompletely ridged and hence incapable of giving full expression to patterns. Ridge irregularities such as those shown in figure 138 are indicative of contours which might have been associated with a well formed pattern had not the extent of ridge formation been so limited. In contrast to this, *Galago* (figs. 29-32) shows completed "primitive" patterns, whorls and whorl-like designs, on a volar surface which is elsewhere lacking in ridge formation. Comparing *Galago* and *Tarsius*, *Galago* presents a relatively more extensive region in which ridges are lacking, and the ridged areas bear whorls and whorl-like patterns, in contrast to the extreme simplicity of ridge arrangement in *Tarsius*. Which of these two prosimians is more primitive with respect to dermatoglyphics? If whorls be accepted as the index, *Galago* has the claim, but it might be urged that the open fields of *Tarsius* are the primitive configuration, inasmuch as the reading of descriptive affinities among configuration types without regard to pad expression is as convincing when begun at one extreme as at the other. Considering as we do that the whorl is a primitive type, *Galago* is viewed as being far more primitive in its dermatoglyphics than *Tarsius*. In support of the validity of the chosen point of reference it should be recognized that if there be adopted any other sequence of patterns from the more primitive to the more specialized than that beginning with the whorl, an irreconcilable conflict with other standards of taxonomic grouping would result. The gibbon, great apes and man would then be assigned to a group more primitive than the monkeys and most prosimians.

The evaluations of pattern intensity which have been followed in our analyses may be regarded as measures of vary-

ing degrees of elevation and circumscription of fetal pads during the period of ridge differentiation. The maximum pattern intensity of a single configurational field (value 1.0, applying to whorls and S-patterns) reflects the existence during that period of a pad having full qualities of elevation and circumscription. At the opposite extreme, an open field (value 0) represents a configurational resultant of loss of elevation and circumscription of the pad at the stage of ridge differentiation. Between these extremes, the sequence of pattern intensity values represents a sequence of gradations of pad conformation. Most closely related to the complete suppression of those qualities of pads which condition patterns, as distinguished from open fields, is that state which brings about but a slight disarrangement of ridges, such as we have characterized as a "vestige", which may be occasionally recognized as an approach to a specific pattern type and so designated in the original formulations (L vestige, W vestige, S vestige). The term "vestige" has been used because of its wide acceptance and for the want of a term which would be free of its evolutionary implication. We emphasize again that no sense of evolutionary sequence is intended, for if effort were made to identify such configurations as steps in an evolutionary series, it would be first necessary to establish their true nature as vestiges rather than as nascent pattern formations. It is true that real nascency is evidenced in most prosimians and in some platyrrhines; but demonstrable nascency is associated with lack of complete formation of epidermal ridges. When ridges are imperfectly formed the variations in pad characteristics and their varying productions of configuration types, as discussed above, are more or less dissociated. A pad having all the qualities of full elevation and circumscription may, nevertheless, bear an imperfectly constructed configuration, the imperfection being due solely to the discontinuities of ridge formation. Under these circumstances a "vestige" justifies consideration as a nascent pattern; were the epidermis advanced sufficiently to possess completely formed ridges the pattern would have



expressed itself in the perfected form. (In the assignment of intensity values to such nascent patterns no discrimination from other "vestiges" or "degenerate" patterns was made, all being treated in like manner solely on the basis of descriptive configurational character.)

*The whole palm and sole.* In the succeeding discussion of affinities repeated reference is made to evaluations of total primitiveness and modification in single genera and in groups. Some of the gauges of primitiveness and modification already have been introduced, and at this point it is desirable to summarize the criteria. No further comment on the expanse of definitely formed ridges seems to be necessary, nor will the characteristics of volar pads require further explanation. The following additional bases of judgment remain to be outlined; (1) Conformity to the morphologic plan; (2) Grades of total pattern intensity; (3) Comparisons of pattern intensity in regional groups of configurational fields; (4) The proportionate pattern intensities of palm and sole; (5) Asymmetry in pattern intensity.

(1) The degree of adherence to the morphologic plan represents a fundamental measure of primitiveness, being a measure of features which are phylogenetically ancient and widely distributed among mammals. Conformity to the morphologic plan never is absolutely complete; usually several configurational areas are not indicated. The chief reliance in the comparisons is placed upon the following configurational fields of the border series —  $H^p$ ,  $H^d$ , Th, I, II, III, and IV — because it is these which are most consistently present throughout the primates. The criteria of conformity to the plan do not concern the presence or absence of patterns as distinguished from open fields, nor do they involve the types of patterns; such variables are taken into account in the consideration of pattern intensity. Lack of conformity to the basic plan is evidenced by the failure of boundaries between configurational fields, usually clearly associated with some specifically identifiable modification of volar pads, blending of two pads into one or lowering to the point of extinction of pad reliefs. Since it

is impracticable to reduce the conformities and non-conformities to a quantitative basis, their comparisons utilize general impressions gained by inspection.

(2) In each genus the average pattern intensities of each of the seven configurational areas listed above, added to give the value known as total intensity, provide a second measure of primitiveness. High pattern intensities indicate not only that the several configurational fields are likely to be individually present in conformity to the basic plan, but also that the areas tend to bear patterns which are either primitive or but little advanced. Intergeneric comparisons may thus be made of the whole palm and sole, separately or combined. When pattern intensity is used in gauging primitiveness, and this applies not only to the total intensities but also to various other considerations of this measure, it must be understood that pattern intensities fluctuate in accord with membral and regional specializations. Because this is true, man, for example, is far from being as nearly primitive with respect to pattern intensities as in the conformity to the morphologic plan of configurations. Indeed, man is to be ranked among the highly specialized primates, along with *Tarsius*, *Ateles* and *Hylobates* — each having its own kind of specialization, in the instance of *Hylobates*, at least, representing departures from primitiveness which are carried further than in man and in directions which are in part peculiar to the genus.

(3) On the assumption that the theoretically most primitive state would take the form of highly developed patterns in all seven of the configurational areas in both palm and sole, comparisons of pattern intensity are designed to disclose evidences of regional unlikenesses. Two modes of regional grouping are chosen, the first being based upon relationships to the anatomical axis. Alongside the axis are the thenar group of configurational areas (Th, I and II) and the hypothenar group ( $H^p$ ,  $H^d$  and IV). In a theoretically unspecialized member the two groups should be equal, each having an intensity of 3.00. With unequal specialization in these outer and inner regions of the same member, the intensities would

be lowered in one group more than in the other, and in comparing the corresponding regions of different members their unlikenesses in pattern intensity would reflect membral specialization.

The second mode of regional grouping separates three sets of configurational fields arranged in disto-proximal sequence: a distal set (II and IV), an intermediate set (I and  $H^d$ ) and a proximal set (Th and  $H^p$ ). In the theoretically most primitive state, the intensities of these three groups would be equal, but our observations indicate that the presumably most primitive condition actually manifested is one in which the intensity of the distal set is greater than that of the intermediate, which in turn is greater than the proximal set. The expression of such a gradient in pattern intensities is based upon progressive specialization in a disto-proximal direction, just as in the thenar and hypothenar groups specializations on one or the other side of the anatomical axis are indicated by lowered intensity.

The third interdigital configurational field, not included in either of the groupings just described, needs no special discussion as to the criteria of primitiveness, inasmuch as it is a single area; specialization of the region, as elsewhere, is associated with lowered pattern intensity.

(4) As for comparisons of total pattern intensities in palm and sole, it is assumed that the ultimate primitive condition would be equality of these members in having the maximum possible intensities. Actually, equality is not observed, except in *Pan*, where it is the result of equal specialization indicated in correspondingly lowered intensities. It is possible that some factor associated with cephalocaudal gradients is responsible for the characteristically greater pattern intensity of the palm, but it is assumed that unusually wide differences are associated with unlike membral specialization.

(5) Since bilateral asymmetry is a widespread phenomenon and the agencies of its different expressions are not identifiable, it would be unwise to select a particular degree of asymmetry as a standard of primitiveness. However, the position

may be taken as a working principle that the lesser grades of asymmetry are primitive, this position being strengthened by the usual coincidence of diminished asymmetry with other dermatoglyphic indications of primitiveness.

## AFFINITIES AMONG THE PRIMATES

### PREMISES

One of the chief objectives of this study was to test the usefulness of dermatoglyphics as indicators of affinities among the primates. This question can not be opened without first taking into consideration several matters concerning both the character of the material and biological attributes of the dermatoglyphics.

When dealing with features having a high degree of individual variability, in which comparisons depend largely upon statistical trends, it is self-evident that sufficient numbers should be available to encompass a representative mass of variations. Even when the number in a single genus is relatively large it should not be assumed that all possible variants will be displayed, and when the number is small the greater caution is demanded in drawing conclusions regarding the dermatoglyphic characteristics of the genus. In a group such as Old World monkeys, wherein a rather consistent dermatoglyphic expression is observed from genus to genus, greater weight may be attached to observations on small numbers. In contrast, genera so highly variable as *Gorilla* or *Pan* call for a larger number of observations to warrant generalization.

The material representing a genus is variably composed of one species alone or of two or more species. No attempt has been made to compare species within a genus. It is possible, even probable, that species differences exist, though such differences would seem to be of little consequence in forms below the apes and man, owing to the greater stability of their pads. In higher primates the pads, and hence the dermatoglyphics, are more variable individually and the possibilities of specific differences (e.g., between *Gorilla gorilla*

and *G. beringei*) are increased. The likelihood of specific differences is strengthened by the existence of sometimes marked differences of dermatoglyphics in human races, though without having large series of specimens it is impossible to demonstrate the distinctions of species. Certainly it is true that differences may occur even in genera otherwise closely related. *Symphalangus*, for instance, is distinguished from *Hylobates* by a much higher pattern intensity in the plantar  $H^p$  and  $I$  areas, as well as more abundant calcar patterns. (The dermatoglyphic distinctions of these two genera further enforce the gap between them which is emphasized by Schultz, '30, on the basis of skeletal characters.)

Since the characteristics of dermatoglyphics are known to be inherited in man, it may be taken for granted that the same genetic principles apply in other primates. Hence it is conceivable that "racial" distinctions in a species of non-human primate might be evolved in a particular habitat, just as a human family may show trends distinguishing it from the general population of the same race and nation (Cummins and Steggerda). It might happen, therefore, that a local collection of specimens would differ from a series obtained in another region. We have not determined the sources of specimens used in this study, since even with this information the comparison of animals from different localities would be precluded by limitations of number, as it is even in the case of species.

All the foregoing points must be kept in mind, and, since the material must be handled as it is or not at all, the only corrective for inadequacies is due caution in drawing conclusions.

The affinities of primates are to be traced in the light of the mechanisms which condition the configurations of epidermal ridges. These mechanisms have been discussed and it is now necessary to examine in greater detail the rôle of volar pads in the evolution of particular dermatoglyphic configurations.

The volar pads in adult primates attain their highest development in some prosimians and in most of the monkeys.

Pongidae and Homo are generally characterized by lowered pads, far less marked than in monkeys though not so reduced as in Hylobatidae. Such variations, together with the local peculiarities involving single pads, are doubtless associated with functional specializations. The influences which modify pads are regarded as the primary evolutionary agency, while the secondary responses of dermatoglyphics to the modifications of pads are thought to be of negligible moment in the evolutionary process. It is apparent that the elaboration of epidermal ridges and the progressive spreading of areas bearing ridged skin may have real significance in the phylogenetic scale, but specific arrangements of these ridges are questionably adequate as primary foci of evolution.

In analyzing the functional significance of volar pads it seems safe to take the position, with Whipple and others, that their primitive functional service is concerned with walking. Volar pads are distributed widely among the orders of mammals, both marsupial and placental. The carnivores may be selected as typical of the walking mammals having pads, and it is this group which is referred to as a standard of pads which are not ordinarily used in prehension; the pads of these strictly walking mammals are lacking in dermatoglyphics. The consistency of the pads in carnivores generally is much firmer than in animals in which prehension assumes an appreciable rôle, and the pads are much more prominent and discrete. Modifications of the morphologic plan occurring in carnivores take the form of fusions of adjoining pads or the loss of components of the plan in company with deviations from pentadactyl construction of the member. Emphasis should be given the fact that different representatives within the same order of mammals may be unlike with regard to the use of the members and the character of the pads. In the carnivores, for example, there are some forms, such as Procyon, which use the anterior members to a large extent in prehension as well as walking. Here the pads present a modification of a different kind. They are lower than the pads of carnivores generally, less discretely outlined at their

bases and are somewhat more yielding, closely resembling the conditions of pads in monkeys with pronounced walking habit.

In primates there is extreme diversity with regard to modifications of pads. Never are these eminences, except in some prosimians, so prominent and so discrete as in typical quadrupeds. The outstanding modifications are lowering or complete suppression, and fusions of adjoining pads. Also in primates the pads are more yielding than in typical quadrupedal mammals. The lowering and yielding consistency facilitate the prehensile use of the member. The dermatoglyphic variations in primates are reflections of modifications of the pads, though it is in the fetal period that the impress of the relationship between pads and dermatoglyphics is effected. Individual configurational variation is reduced to a minimum in primates which retain conspicuous pads in the adult, and in those forms which may be assumed to have passed through a much accelerated subsidence of pads in the fetal period (*Hylobates*). These reductions of individual variability are associated with the utmost stability of volar pads in the fetus, in the one instance expressed as the maximum retention of fetal pads and in the other the maximum and earliest suppression. Since there must exist some degree of chronological variation in subsidence of pads, such variation would be expected to reach its extreme in those forms which present only slightly marked pads in the adult, as in *Gorilla*, *Pan* and *Homo*. The known history of regression of pads in the fetal period of man suggests that the pads are involved in a still active phase of phylogenetic involution. If this be true, the high individual variability in the regressive behavior of pads in man, and assumedly in *Pongidae* as well, is comparable to the variability of other anatomical features that are developmentally labile because of their involvement in an uncompleted evolutionary process. That is to say, such pads, being neither completely retained in further development, nor totally suppressed prior to ridge differentiation, should be quite inconsistent at the time of ridge differentiation. That this is the

case is borne out by an actually high dermatoglyphic variability in Pongidae and Homo. Accordingly, our analysis of dermatoglyphic variation represents an evaluation of the state of the pads only during the formative period of the dermatoglyphics. There is probably an essential correspondence in the fetal and adult characteristics of pads in those primates which exhibit the most prominent pads in the adult (some prosimians and most monkeys).

If the volar pads are to be regarded as primitively associated with walking, then their attainment of softer consistency and their subsidence are modifications attending the acquirement of the prehensile function, either supplementing or superseding the original walking function. It may be assumed, even in the absence of observations on the fetuses of all primate genera, that there is variation among them in the chronology of pad development. In a form presenting earlier and more nearly complete suppression of the fetal pads the inference is that this form stemmed from an ancestry of walkers at a period earlier than the splitting of the line leading to forms which retain pads for a longer period of the fetus; these forms in turn would be phylogenetically farther removed from the common ancestry than primates which retain permanently well defined pads.

The foregoing deductions would be invalidated if it were proved that the pads are not subject to Dollo's principle of the irreversibility of evolution. It is conceivable, though not demonstrable, that volar pads, having undergone the modifications brought about by arboreal existence and prehension, might be restored to original primitiveness by resumption of the walking habit. Since observations on human fetal pads indicate that pads having primitive qualities appear temporarily, the pads should not be considered as irrevocably suppressed even in a form presenting but little indication of them in the adult. It might be even conjectured that in a form such as man the greater retention of primitive characteristics of fetal pads in the sole is a result of newly acquired walking habit, the acquisition coming too late in the evolu-



tionary sequence to bring about permanently elevated pads, but early enough to influence a more prolonged fetal retention. Following the same line of conjecture, the Old World monkeys might have stemmed from an arboreal stock at a period so early that the pads still possessed all the potentialities necessary to regain full primitiveness even after they had been modified under the circumstances of arboreal life. In our consideration of primate affinities resort has been made only to descriptive standards of primitiveness, inasmuch as it is impossible to evaluate these speculations and to determine whether a descriptively primitive condition is primary or secondary.

The processes of ridge differentiation in the fetus are of such nature that specific configurations are mere by-products, their qualities fluctuating in accord with the ontogenetic mechanisms which determine them rather than being regulated by factors which are associated with the configurations themselves. What constancy there is in the configurations is the correlate of the degree of constancy in the reliefs of the surface. We have dealt principally with configurations which are identified with volar pads. It is the systematic topography of these pads which accounts for the existence of the dermatoglyphic plan, and all departures from that plan may be readily explained on the basis of varying behavior of the pads at the time of ridge formation or prior to it. If the variations of the palmar and plantar dermatoglyphics were not restricted by the limits of variation of the pads, their expressions of specific configurations on the palm and sole would show no systematic order. With no local irregularities of relief at the time of ridge differentiation, the configuration would be as monotonous as that shown in a sole of gibbon (fig. 499), neither patterns nor vestiges being present to disturb the expanse of this continuous open field. Were there unsystematic irregularities of contour the surface might on the other hand be marked by erratic local patterns and ridge disturbances resembling those seen in the tail of *Lagothrix* (figs. 594, 595).

In man there are well recognized dermatoglyphic differences among races, as well as sexual, bimanual and constitutional distinctions. Though references are not cited, the details being of no importance in this discussion, an illustration is offered in the frequencies of whorls of the fingertips in different races. The lowest known frequency of whorls, 19% of all fingertip patterns, occurs in the *Efé* pygmies of Africa. The Eskimos of Eastern Greenland present, in contrast, a frequency of 72% whorls. Many other examples of wide differences among races might be mentioned. It is hardly likely that different races of mankind would be so markedly divergent as a result of an evolution dependent upon the greater frictional or tactual serviceability of one type of configuration over another.

There is a close parallelism between dermatoglyphic configurations and hair direction. Hair direction, as studied in the human fetus (Ludwig, '21), presents configurations which may be likened to the characteristics of dermatoglyphics. Among other correspondences there are hair streams over large areas which simulate open fields, vortices which compare to patterns, and junction points between hair systems which find their counterparts in triradii. As another point of likeness, the hair directions are determined by mechanical factors in fetal growth, and they are subject to individual variations of the same fundamental nature as the variations in dermatoglyphics. Skin folds and stripes of pigmentation (Krieg, '21) and various other parallels with dermatoglyphic principles also might be mentioned in support of our interpretation that the dermatoglyphics are inadequate as an effective primary evolutionary medium. In our opinion a specific configuration of epidermal ridges is no more significant from this standpoint than is a specific configuration of hair direction or a particular pattern of striping on the forehead of a zebra.

Though studies are not yet available for an all-inclusive survey of the primates with reference to the fetal history of volar pads, it may be assumed that the dermatoglyphics

represent a record of the pad characteristics at the time of ridge formation. In man that period is at the close of the first trimester of gestation and the beginning of the second. Whether other primates would undergo the critical phases of ridge differentiation and pad development at a relatively equivalent period can only be conjectured. It may be repeated that the comparison of dermatoglyphics among genera is intrinsically a comparison of fetal volar reliefs, reliefs which are variably retained or modified in the adult.

#### GENERIC AND GROUP COMPARISONS

Most of the following comparisons are confined to genera represented by reasonably adequate numbers of specimens. The best introduction is provided by Old World monkeys, the only group in which the several genera studied are fairly uniform in their characteristics. These characteristics indicate generalization, or primitiveness. Prosimians, New World monkeys and great apes are not considered collectively as groups because there is no such consistency among their genera.

*Old World monkeys.* This group comprises the most pronounced walkers. It is therefore perhaps not unexpected that the prevailing characteristics of dermatoglyphics are of the type associated with a high development of pads. Ridges are continuously formed except that small areas of imperfect ridge structure are occasionally noted in some Colobinae. Departures from the morphologic plan of configurational areas are at a minimum, the most important being the frequent merger of Th and I. Total pattern intensity is high both in palm and sole. There is but little difference between hand and foot in their total intensities, and the existing difference is in the same direction as in non-human primates generally, the higher value being in the palm. Pattern intensities of the hypothenar and thenar groups of configurational fields, both in palm and sole, are substantially equal, as are the groups in the palm compared with the regionally corresponding groups in the sole. The relative pattern intensities of the three disto-

proximal groupings of configurational fields are fairly consistent among the genera, the distal group being greater than the intermediate, and that in turn usually greater than the proximal group. There is relatively little bilateral asymmetry in pattern intensity; the tendency for excesses in pattern intensity to favor the left side is exceptional. The regional distributions of configurational fields showing dextral and sinistral excesses in pattern intensity are virtually corresponding in hand and foot.

It has been indicated that all the genera conform closely to the same dermatoglyphic description. The only noteworthy failures to agree fully with the group characteristics are observed in the Colobinae, with *Pygathrix* as the representative mainly figuring in the comparison because of limitations of material in the other genera of this subfamily. In *Pygathrix* is to be found the lowest pattern intensity of the Old World monkeys, while the excess of hand over foot is the most marked. Also, there is more pronounced bilateral asymmetry than in other catarrhine monkeys. (The dermatoglyphic distinctions of *Pygathrix* are thus to be added to the considerable list of anatomical characters — Washburn, '41 — in which the genus differs from the usually accepted attributes of Old World monkeys.)

The Old World Monkeys, with the exception of *Pygathrix* (and perhaps the other Colobinae), are but little specialized. It can not be asserted that these monkeys form a main trunk in the genealogy of dermatoglyphics, but this much is certain: the Old World monkeys as a group embody all the acceptable indicators of dermatoglyphic generalization, and they display even exaggeration of one sign of primitiveness, large expanse and high elevation of pads.

*Lemuroidea*. In contrast to Old World monkeys, the prosimian genera present wide diversity in dermatoglyphic traits and in locomotor habits.

*Galago*, of all the genera examined, exhibits greatest primitiveness. The palm and sole alike present extensive areas in which ridges are not formed. The pads and configurational

fields conform closely to the basic plan. Galago presents the highest pattern intensity of all prosimians, and the excess of palm over sole in pattern intensity is small; differences of intensity among the configurational groups and between right and left members are slight.

Nycticebus is definitely less primitive than Galago in the following respects: the extent of formed ridges is increased to the point of completeness in the case of the sole and in some palms (which otherwise lack complete ridges only in a very small area); pattern intensity is lessened; there is increased difference between the pattern intensities of the palm and sole; increased regional differences in pattern intensity occur.

The attempt to place Daubentonia, Tarsius, Perodicticus and Lemur in a sequence of decreasing primitiveness might lead to a spurious order. Lemur, for example, is not as advanced as Nycticebus with regard to the extent of completely ridged skin; but paradoxically there is a greater advance as measured by the distinction of the palm and sole in pattern intensity, and resemblance to the configurational topography of the simians is striking.

Perodicticus may be assigned an intermediate position between Galago and Nycticebus. The ridged area, as compared to Galago is greater in expanse, and the configurational fields closely approach the appearance of Nycticebus. Further comparisons are not feasible because of the availability of only a single individual.

The placing of Tarsius presents a problem. The dermatoglyphics, primitive in view of the large expanse of ridgeless skin, are advanced in the modifications brought about by fusion of pads and configurational areas, and in regional disparities in pattern intensity. On the basis of pattern intensity and according to the interpretation which is applied elsewhere, Tarsius would be described as advanced also in possessing a low pattern intensity, indeed the lowest of any primate. The qualities of the pads and configurations lead inescapably to the impression that Tarsius represents a unique departure from the characteristics of all other primates.

These observations, therefore, support evidences drawn from other features toward the separation of the Tarsiidae as a distinct group. We can extract from the dermatoglyphics of *Tarsius* no indications that this form stands in the line of evolution of the higher primates.

*New World monkeys.* Most platyrrhines contrast with Old World monkeys in their characteristic arboreal life and in the locomotor habits which are associated with it. One of the most active brachiators, *Ateles*, is a member of the group. From the standpoint of dermatoglyphics they are heterogeneous, in this respect also differing from the fairly consistent traits of Old World genera.

Callithrichidae display dermatoglyphic features which are fairly uniform among the four genera observed. The family is accordingly a more unified group than Cebidae, wherein the diversities mentioned above are concentrated. With regard to the extent of fully formed ridges, Callithrichidae retain some measure of primitiveness. In the palms of *Seniocebus*, *Leontocebus* and *Oedipomidas*, but not in *Callithrix*, the distal portion of the central area presents a lack of definite ridge formation. The proximal portion of the heel region, in at least some feet of all four genera, is devoid of formed ridges (as if the pelage of the corresponding region of *Lemuroidea* had but recently disappeared and ridge formation had incompletely progressed into the region last depilated). Retention of a ridgeless region in the central area of the sole is rare, being noted in only one sole (*Leontocebus*, fig. 47). The family is fairly primitive with respect to the expressions of the basic morphologic plan of patterns, but pattern intensity is lower than in some Cebidae (*Alouatta*, *Saimiri* and *Aotus*), and the difference between palm and sole is greater than in the same genera.

The six genera of Cebidae may be conveniently grouped for description: (1) *Saimiri*, *Cebus*; (2) *Aotus*; (3) *Lagothrix*, *Alouatta*; (4) *Ateles*.

*Saimiri* and *Cebus* are mentioned first, inasmuch as the dermatoglyphic characteristics are close to those of *Calli-*

thrichidae. The advance of ridge formation, especially in *Cebus*, is greater than in *Callithrichidae*, and the frequency of individuals presenting incomplete ridge formation is lessened. In *Saimiri* and *Cebus*, especially the former, pattern intensity is higher than in *Callithrichidae*. The excess of pattern intensity in the palm is less in *Saimiri* than in *Cebus* or the *Callithrichidae*, and in this respect, as well as in the higher total intensities, *Saimiri* is more primitive than the *Callithrichidae* or *Cebus*.

The greatest primitiveness to be found in New World monkeys is observed in *Aotus*: a large expanse of unridged skin; a high pattern intensity; slight difference in pattern intensity between palm and sole; a nearly perfect adherence to the basic morphologic plan of pads and patterns (so nearly perfect, in fact, that this genus has served constantly as a reference standard).

When compared with the New World monkeys previously mentioned, *Lagothrix* and *Alouatta* represent a greater advance with reference to complete ridge formation. As signs of primitiveness, however, both genera show high pattern intensities, and they present frequent indications of central patterns. *Alouatta* displays a smaller difference between palm and sole in pattern intensity, in this being less specialized than *Lagothrix*. Both genera have prehensile tails which bear dermatoglyphics, a trait which they share with *Ateles*.

*Ateles* is the most highly specialized representative of the New World monkeys, and it seems quite probable that its dermatoglyphic specialization may be correlated with the brachiating habit. Morphologically the palm is distinctive; it is elongated and there is a broad V-shaped configuration including and surrounding the parathenar area. (This V-shaped configuration, as well as the occurrence of palmar patterns, is conspicuously different from the appearance of the dermatoglyphics in another pronounced brachiator having a similarly elongated palm, *Hylobates*.) The extreme reduction in pattern intensity of the third interdigital area of the palm is a unique exception to the trend among all monkeys,

though it is matched or closely approached in other brachiators — *Hylobates*, *Pongo* and *Pan*. A similar situation obtains, curiously enough, in the soles of the same genera, also in *Symphalangus* and in *Callithrix* (notwithstanding that *Callithrix* is a non-brachiating primate and that the sole would not be concerned in brachiating suspension).

In examining the eight genera of New World monkeys for the difference between pattern intensities of palm and sole, the comparison may be made conveniently with the use of a palm/sole index of pattern intensity, supplementing the graphic record shown in figure 597. An index of 100 indicating equality, *Aotus*, *Alouatta* and *Saimiri* (with respective indices of 112, 113, and 118) present relatively small excesses of pattern intensity in the palm. *Callithrix*, *Oedipomidas* and *Lagothrix* (with indices 137, 147, and 150) show considerably greater membral difference, while *Cebus* (168) and *Ateles* (191) show still greater difference. It has been stated previously that the Old World monkeys present little difference in pattern intensity between palm and sole, and at this point the actual indices may be listed for ready comparison with the New World monkeys: *Cercocebus*, 92; *Lasiopyga*, 106; *Papio*, 108; *Pithecius*, 114; *Erythrocebus*, 114; *Pygathrix*, 136. This exceptional position of *Pygathrix*, with regard to large difference between palm and sole, is not alone in rendering this genus a distinctive member of its group; there are other outstanding departures, as noted previously and below.

The palm and sole of New World monkeys show small differences between the corresponding thenar and hypothenar groups of configurational areas, and the greatest difference observed in comparing the two groups in the same member is found in *Ateles*. Crossed comparisons of the thenar group in the palm and hypothenar group in the sole show wider differences in *Oedipomidas*, *Ateles*, *Lagothrix* and *Cebus* than in other genera, *Ateles* being the most distinctive in this respect. With regard to the distal, intermediate and proximal groups of configurational areas (fig. 601), the platyrrhines show two different trends of interrelationships in the palm and sole.



Examining first the palm, some New World monkeys (*Aotus*, *Ateles*, *Lagothrix* and *Cebus*) resemble the Old World monkeys in presenting a disto-proximal gradient in pattern intensity. The *Callithrichidae* and *Alouatta* (with *Saimiri* as an intergrading form) present relationships which are like those in certain prosimians, where the gradient relation is disorganized. In respect to the sole, *Lagothrix* and *Cebus* are exceptions to the general trend in monkeys, in which there is conformity to the disto-proximal gradient. In these two genera it is the intermediate group which presents maximum intensity rather than the distal group. The only other exception occurs in *Pygathrix*, which, as noted above, is in other respects a non-conformist to trends in Old World monkeys.

The New World monkeys are more asymmetrical than Old World monkeys (with the exception of *Pygathrix*) in the pattern intensities of right and left sides (table 9). The platyrrhines show consistently more asymmetry of the sole than of the palm, while in Old World forms there is a tendency toward reversal of this relationship. In the New World monkeys pattern intensity is characteristically greater in the palms and soles in the right side; in Old World monkeys there is a reversal of this relationship which is consistent in the palms of the four genera but inconsistent in the soles. The relative asymmetry of the palm varies among the four genera of New World monkeys in which the numbers available admit analyses of asymmetry. *Alouatta* may be regarded as the most primitive, both because the total asymmetry is less than that in *Saimiri*, *Ateles* and *Cebus*, and because palm and sole are about equally asymmetrical. In this feature *Alouatta* is inclined toward the catarrhine monkeys.

*Gibbon*. *Hylobates*, the most extreme of all brachiators, has the most specialized dermatoglyphics yet considered. The elongated palm is distinguished by an almost strictly longitudinal coursing of ridges, the character of the longitudinal system being accentuated by the prevailing absence of patterns except in the extreme proximal region. The first interdigital interval is extended far proximally, isolating from

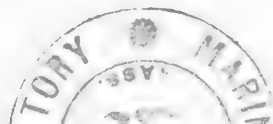
the palm proper the zone of the first metacarpal and the associated first interdigital configurational area. The intensity of patterning in the palm and sole is the lowest in all the simians, and there is pronounced modification of the fundamental plan of dermatoglyphics. There is a marked difference of pattern intensities of palm and sole (index 143, which is close to that of several New World monkeys). The thenar and hypothenar groups (see fig. 600) show reversed tendencies in the intensities of pattern of palm and sole, the palm having a higher pattern intensity in the hypothenar group and the sole a higher intensity in the thenar group. The pattern intensities of the three transverse groups of configurational fields present, as compared to Old World monkeys, a reversal of the relative intensities of distal and proximal groups both in palm and sole. While the total asymmetry in gibbon is much higher than in any of the monkeys, the relationships of members of the two sides, as indicated in the asymmetry index, conform to the generalizations set down for the New World monkeys. The magnitude of bilateral asymmetry is much higher than in any monkey, though the proportionate asymmetry in palm and sole is like that of most monkeys, and is much lower than is the case in the great apes and man.

*Great apes and man.* Sharp differences in locomotor habits and modes of existence occur among these four genera. All the great apes are partly arboreal, and man is at least potentially so. "The orang-utan spends practically his entire life in the trees, the chimpanzee, though an expert in trees, spends a good deal of time on the ground, and the gorilla is by far the least arboreal great ape, the enormous adult males ascending trees but rarely." (Schultz, personal communication.) Taking into account all dermatoglyphic criteria, Pongo, the most arboreal, and Homo, the most terrestrial form, may be assigned respectively to the lower and upper extremes of specialization, Pan and Gorilla being intermediate. With regard to adherence to the basic plan of dermatoglyphics alone, Pongo and Homo are unquestionably the least specialized, while Gorilla and Pan are the most highly specialized

genera; it is difficult to establish the relative positions of Gorilla and Pan in a scale of increasing modification of the plan.

By combining the pattern intensities of palms and soles, and considering that decreasing pattern intensity is an evidence of specialization, the order from the more primitive to the more advanced is Gorilla, Pongo, Pan, Homo. Considering the hand separately, the series is Pongo, Gorilla, Pan, Homo, while the order of the foot is different: Gorilla = Homo, Pan, Pongo. It is evident, therefore, that palm and sole have proceeded differently in the course of involution of pattern intensity, and that the soles of Gorilla and Homo, the two primarily terrestrial genera, retain a larger measure of primitiveness. In Pongo and Homo the palm shows a significant deviation from the pattern intensity of the sole. In man the plantar pattern intensity is over twice that of the palm; in Gorilla and Pan the plantar and palmar intensities are essentially equal, contrasting with conditions in Pongo where the palmar intensity is 70% greater than that of the sole. Special emphasis is due this relationship of palm and sole in Pongo, the only great ape presenting a significantly smaller pattern intensity in the sole. In its conformation the foot of Pongo is more hand-like than the foot of any of the simians, and it is possible that the foot serves to a larger extent in prehension. At any rate, the sole in Pongo has less significance as a contact surface in walking since the animal walks on the outer borders of the feet.

The soles of Gorilla and Pan show negligible difference in the pattern intensities of the thenar and hypothenar groups of configurational zones, while Pongo and Homo evidence a much greater intensity in the thenar than in the hypothenar group. These group intensities behave quite differently in the palm; Pongo and Pan show but little difference in the intensities of the two groups, the excess being in the thenar. Gorilla and Homo present marked pattern intensity differences in the two configurational groups, and here it is the hypothenar group which bears the larger intensity. In all



four genera there is a considerable spread between the pattern intensities of palm and sole in these group combinations, the spread reaching its maximum in *Homo* and being least in *Pan*.

The three transverse groupings of configurational fields of the palm, arranged in order of decreasing pattern intensity, show in *Pongo* an approach to the relationship observed in *Hylobates*. In *Hylobates* the order is proximal > intermediate > distal. The relations in *Pongo* are proximal > distal > intermediate, while in *Gorilla*, *Pan* and *Homo* the order is altered to distal > proximal > intermediate, this order being a lesser degree of departure from conditions in the Old World monkeys. In the sole the sequences of the groups are much less consistent among the apes and man. *Pan* presents the same order as *Hylobates*. The variable relationships of these configurational groups in *Pongo*, *Gorilla* and *Homo* may be noted in figure 601. Here as in other comparisons, the palm evidences more orderly relationships among genera than does the sole.

Differences in pattern intensity between right and left sides are least in *Pongo* and *Homo*, greatest in *Gorilla*, and intermediate in *Pan*. In the palm these asymmetries, in terms of excesses of pattern intensity in corresponding configurational areas, are shared about equally on right and left sides only in man, while in the human sole the relative excess of asymmetry on the right side is greater than that of any of the great apes, indeed greater than in any other primate studied. In man the relative asymmetry of the hand, that is to say the contribution of the palm to the combined dermatoglyphic asymmetries of palms and soles, is by far greater than that occurring in any other primate; *Pan*, *Gorilla* and *Pongo* follow in the order of decreasing relative asymmetry of the palm. The completion of this series with *Pongo*, in which there is more asymmetry in the sole than in the palm, arrives at a relationship which is about that of monkeys and gibbon.

With special interest centering on the affinities of man, in this instance the evidences of the dermatoglyphics call for

further discussion. In their comparative surveys of primate dermatoglyphics, Whipple, Schlaginhaufen, Wilder and Bychowska attempt to establish the descent of man. A detailed presentation of their conclusions is considered unnecessary. The approach here followed is in most respects quite new, and we omit such details as being in a class with analyses which deal with other anatomical criteria unrelated to the present approach.

No single line of comparison can be established with certainty as the most significant. The collective resemblances agree with other signs indicating that man is more closely related to the great apes than to other primates. According to some dermatoglyphic criteria man resembles most closely Pan, in others Gorilla, and in still others, Pongo. Man is most closely related to chimpanzee on the basis of total pattern intensities, relationship of pattern intensities between palm and sole, and relative asymmetry of the palm. It is our judgment, though we are unable to assign relative values to the resemblances in other features of Pongo and Homo and of Gorilla and Homo, that the criteria which ally chimpanzee and man are of greater weight. This is not to be taken to mean that any one of the great apes might represent an ancestral type leading to man. As a matter of fact, the dermatoglyphics suggest two lines of evidence contraindicating this conclusion. In the first place, it appears that man must have arisen as an offshoot from a primate stock lower in the scale of dermatoglyphic specialization than that of any recent ape. The palm is especially useful as a source of evidence, showing as it does in man general ridge directions which, instead of being longitudinal as in the apes, are more like the transverse trends observed in monkeys. (Notwithstanding that palmar dermatoglyphics of thousands of individuals have been examined, by various workers, only one instance is known in which the general ridge courses assume the longitudinal character typical of the apes. Wilder, '16.) Secondly, both palm and sole of man, and in spite of the peculiar modifications in the form and anatomical construction of the foot, adhere closely to the

primitive morphologic plan of the configurations, more closely than any of the great apes. The retention of this primitiveness is especially evident in the distal portions of the palm and sole. It is of interest to note that Pongo, the ape which most nearly resembles Homo in reference to retention of the primitive plan, is much farther from the primitive in the sole than in the palm, while in man this aspect of primitiveness is about equally distributed in the two members. As pointed out previously, we have regarded likeness of hand and foot as indicating primitiveness or equal advance in specialization of the two members. While in man both palm and sole present some modification of the basic plan, both members are unquestionably more primitive than the sole of Pongo. It seems quite probable that man and the great apes sprang from a common stem, man being closer to the primitive, as noted above, each genus then proceeding along an independent line of dermatoglyphic specialization associated with differential locomotor and prehensile uses of the members and the attendant unlike gross structural modifications. As based upon the total pattern intensities of palm and sole, it is suggested that Pongo retained the characteristic functional membral distinctions of the ancestral type, and that these distinctions were progressively obliterated in Gorilla and Pan, and reversed in Homo, where the sole rather than the palm presents the higher intensity. The primitiveness of the sole, as indicated in high total intensity as well as close adherence to the morphologic plan, may be credited to the retention (or acquisition) of the walking habit. In Gorilla and Homo there would have been similar evolution in the uses of the soles, hence in their pattern intensities. The palms of Gorilla and man, in contrast, must have proceeded along divergent courses, that of Gorilla retaining a larger share of original primitiveness and that in man becoming in many respects highly specialized. This dissociation of palm and sole in evolutionary sequence did not occur in chimpanzee, where palm and sole were equally involved in reduction of

pattern intensity and in divergence from the morphologic plan.

It has been shown that the uncertainties surrounding an inquiry into the affinities of man arise in part from the independence of evolutionary sequences involving different dermatoglyphic traits. This independence has been pointed out in preceding sections, and it may be recalled that it extends to the very beginnings of dermatoglyphic evolution, being illustrated in advances of areas of ridged skin and involution of patterns on volar pads. In the same manner departures from the morphologic plan of configurational fields, reduction of total pattern intensity, the reductions of intensity in individual configurational fields and groups, and expressions of asymmetry in pattern intensity, all seem to advance more or less independently rather than in a mass departure from primitiveness. The frequent unlikeness of evolutionary progress in palm and sole is another and an important illustration of this principle of independence.

It is apparent that specializations of members and of regions are associated with responses in the dermatoglyphics. These responses may vary widely among genera within the same taxonomic group, as in great apes or New World monkeys. In consequence, it follows that the membral and regional specializations may so alter the dermatoglyphics that their traits come to be indicative of varying uses of members rather than or in addition to genetic affinities. There are suggestions of convergent specializations within different taxonomic groups, most comprehensively represented in the prosimians, New World monkeys, and even the marsupials. The convergent specializations often closely correspond among genera belonging to different groups, and the existence of like directions of specialization within different groups suggests that parallel or convergent evolution in dermatoglyphic features (influenced by similar functional adaptations of the members) is an actual phenomenon. The resemblances among *Ateles*, *Hylobates*, *Pongo* and *Pan*, which may be explained on the basis of brachiation, may be recalled as an illustrative example.

## SUMMARY

1. This study was designed as a search for evidences bearing on morphological principles of dermatoglyphics and to test the value of dermatoglyphics as indicators of affinities among the primates. The material comprises, in addition to extensive records of human dermatoglyphics, the palms and soles of thirty-five genera adequately representative of both prosimians and simians.

2. Ridge-bearing skin is essentially continuous over the whole palm and sole in Old World monkeys, gibbon, great apes and man. In New World monkeys and in prosimians there exists wide diversity in the extent of definitely formed ridges. Ridge-formation, an advance in epidermal specialization, is confined primitively to the summits of volar pads. The ventral surface of the terminal portion of the tail in three New World monkeys (howler, spider monkey, woolly monkey) is similarly specialized. Ridging of volar and caudal skin enhances friction in contact and gives increased acuity of the tactile sense; there is question as to which of these functions, if either, may have been concerned primarily in the evolution of epidermal structure.

3. The breadths of epidermal ridges (in the palmar hypothenar region of thirteen genera) tend to vary inversely with hand length, but the association between ridge breadth and hand size is loosed by the existence of factors which control ridge breadth independently. The unlikenesses of ridge breadth in relation to hand length among different genera exceed the unlikenesses existing in a single genus represented by hand lengths varying according to age.

4. A basic plan of volar pads and of dermatoglyphic fields is presented, supplementing previous schemes by the addition of elements which had been either unrecognized or not systematized heretofore. The plan is an idealized composite, based in part on the dermatoglyphics and the pads as observed post-natally and in part on the pads in fetal stages. The topography of pads and other irregularities of the volar relief coincides



with the topography of configurational fields, and the fields of palm and sole are counterparts in all essentials. The border series of configurational fields includes: distal hypothenar; proximal hypothenar; thenar (separated into distal and proximal elements in the sole); first interdigital; accessory second interdigital; second interdigital; third interdigital; fourth interdigital; and accessory fourth interdigital. The calcar area of the sole represents an extended portion of the proximal hypothenar field. The central configurations are: a series of three small fields forming a sequence in proximal relation to the second, third, and fourth interdigitals; the parathenar configuration, occupying the region between the thenar and hypothenar fields.

All the configurational fields, as listed above, are not individually recognizable in a palm or sole. If the field is patterned, and when patternless if it is discretely bounded, conformity to the plan is clear. Merging of some units in the plan, through suppression of boundaries, is of universal occurrence. The varying departures from the plan are systematically described. The prosimian genera are heterogeneous with respect to departures. Of the remaining groups the New World monkeys present in general the least departures, while Old World monkeys are diverged farther from it, and the higher primates still more. In the higher primates the order of increasing modification is man, orang, gorilla, chimpanzee, gibbon — with a questionable transposed placing of gorilla and chimpanzee.

5. The general courses of ridges in areas distinct from the localized patterned fields vary from longitudinal to transverse, and the trends exhibit no orderly distribution in reference to taxonomic groups. In gibbon and great apes the direction ranges from strictly longitudinal to oblique; in man the palm presents a combination of longitudinal and diagonal, while plantar ridges course transversely or on a slant closely approaching the transverse.

6. By assigning weights to configuration types of different degrees of complexity, a measure of "pattern intensity" is

obtained, this measure being applied in various comparisons. The higher values of pattern intensity indicate greater frequency and greater complexity of patterns.

Summations of the values of the several fields in palm or in sole yield a measure termed "total intensity". The total intensities of both palm and sole in prosimian genera are widely variable. Of the other groups, the Old World monkeys present the highest values. New World monkeys are next in the order of decreasing values; the higher primates, with gibbon having the minimum, present still lower values.

In non-human primates total pattern intensity is higher in palm than in sole, probably indicating greater advance in specialization of the foot. (There are other dermatoglyphic expressions marking greater advance in the foot of non-human primates: more extensive area of formed ridges in genera having incompletely ridged volar surfaces; more accelerated suppression of central pads; the generally greater degree of departure from the basic plan; and, except in chimpanzee, a larger magnitude of asymmetry. Man represents an exception to conditions typical of primates, in presenting a higher total intensity in the sole and in having a plantar asymmetry which is much reduced in comparison with that of the palm; in man, therefore, the sole is in these respects less advanced than the palm.)

The intensities of individual configurational fields are analyzed in detail. Among other findings, it is shown that the elevation of plantar intensity in man is localized in the distal hypothenar field and in interdigitals I, II and III, the interdigital areas alone being exceptional to the trend in non-human forms. The third interdigital area of both palm and sole presents a lower intensity than its neighbors, and the reduction is especially marked in brachiators.

The intensities of interdigital areas II, III and IV indicate that their sequential relations in palm and sole are serially homologous in non-human primates generally, but in the human foot the pattern intensities are shifted in accord with the different alignment of the anatomical axis of the foot.

The pattern intensities of grouped configurational fields also are compared. The combined intensities of the fields on either side of the anatomical axis (thus excluding interdigital III) are compared in the same member, as are corresponding and opposed groups in anterior and posterior members. As a result of all these comparisons showing equality and unlikenesses of group intensities, it appears that Old World monkeys, some New World monkeys, gorilla and chimpanzee are more generalized; the spider monkey, gibbon, orang, and man show the extremes of non-agreement between palm and sole.

The component fields of the two groups considered above are regrouped to form transversely divided sets: distal, intermediate and proximal. The apparently basic seriation is in the form of a disto-proximal gradient in which the groups in the order named present successively lowered intensities. The Old World monkeys and some New World forms typify the gradient. Gibbon, great apes and man exhibit disorganizations of this gradient, varying in kind and degree among the genera.

7. Determinations of pattern intensity are assembled also for comparisons of bilateral asymmetry.

Considering first the asymmetries of individual configurational fields, it is to be noted that in man the right palm shows higher intensities in the proximal hypothenar field and second and third interdigitals, while the remaining fields (thenar, and first and fourth interdigitals) have higher intensities in the left palm. In New World monkeys the topography of fields presenting higher intensities nearly duplicates that in man, with Old World monkeys, great apes and gibbon forming a series of progressive departures from conditions in the human palm. Only in Old World monkeys is there a close parallelism between palm and sole in the disposition of fields showing dextral and sinistral ascendancy in pattern intensity. New World monkeys, gibbon, the great apes and man exhibit greater unlikeness of palm and sole, New World monkeys

being closest to Old World monkeys in this intermembral comparison.

Considering next the aggregate asymmetry expressed in the palm and the sole as a whole, the Old World monkeys, New World monkeys and higher primates form, in the order named, a progression of increasing asymmetry. Of the higher primates, orang and man are the least asymmetrical and gorilla the most asymmetrical, chimpanzee and gibbon being intermediate between these extremes.

The relative asymmetry of palm and sole varies widely. In monkeys the palm presents less asymmetry than the sole, and in the higher primates there is a regular sequence of increasing relative asymmetry of the palm. Gibbon is comparable to the monkeys, having a palmar asymmetry which is only about one-third that of the sole. Orang presents a relative asymmetry twice that of gibbon, though plantar asymmetry remains greater than palmar; in gorilla palm and sole have equivalent asymmetries, while chimpanzee and man continue the series of increasing relative asymmetry of the palm.

8. The consideration of affinities among primates is based upon the following premises. (a) The conditioning of specific dermatoglyphic configurations is a by-product rather than an immediate vehicle of the evolutionary process. The features primarily concerned in the evolutionary process are the volar pads and other gross qualities of form and relief of the member. The dermatoglyphic configurations are reflections of particular forms and reliefs of the members in their fetal development. (b) Prominently elevated and circumscribed volar pads are considered primitive; lowering of pads and obliteration of their boundaries indicate modification incident to prehensile use. Whorls and whorl-like patterns are associates of the primitive condition of the pads, while patterns of lesser complexity and open fields accompany states of regression of pads. In terms of pattern intensity, higher values thus indicate primitiveness. (c) Adherence to the basic plan is a mark of primitiveness and degrees of specialization

are indicated by departures from the plan, including such variants as suppression of individual configurational fields and fusions of neighboring fields. (d) Approach to equally high pattern intensities of the several configurational fields, singly or grouped as described above, is an indication of primitiveness. Likewise an approach to equality in high total intensity values of the palm and sole is evidence of primitiveness. (e) Minor degrees of bilateral asymmetry in pattern intensity are ranked as primitive, and increase in dextral and sinistral differences points to specialization.

Dermatoglyphics are subject to convergences in the evolutionary process. In marsupials and prosimians, for example, the dermatoglyphics cover a range of variation which may be compared closely to that of New World monkeys, and what is more to the point, the specific trends of variation comprised in any one of these groups are closely matched in the others.

The tracing of affinities is complicated by the apparent independence of the structural expressions which give measures of primitiveness and specialization. The different criteria lead to different orders of resemblance and unlikeness among the forms compared. The divergent results are summated, however, in arriving at judgments of relationship.

9. The prosimians are heterogeneous; it should be noted that the dermatoglyphics contraindicate simian origin from a tarsier-like stem. Old World monkeys, with the exception of langur, exhibit least specialization of dermatoglyphics; in respect to expanse and character of patterns, they have even exaggerated signs of primitiveness. The resemblance of langur to some New World monkeys is closer than to other Old World monkeys. The New World monkeys are diverse. The most primitive members are the night monkey and marmoset-like monkeys, the most specialized being the spider monkey. The squirrel monkey and capuchin are neither so primitive as the night monkey and marmoset-like forms nor so specialized as the woolly monkey and howler. Gibbon is the most specialized simian. The three great apes and man present specializations which follow different directions. While

these divergent specializations render comparison difficult, the order of increasing specialization indicated by the pooled evidence is orang, gorilla or chimpanzee, man. Especially in adherence to the basic plan of configurations, man is even more primitive than orang; inasmuch as that plan is so fundamental a characteristic, it is concluded that man stemmed from an ancestral stock more primitive than any recent ape, having dermatoglyphic traits more closely allied to those of monkeys.

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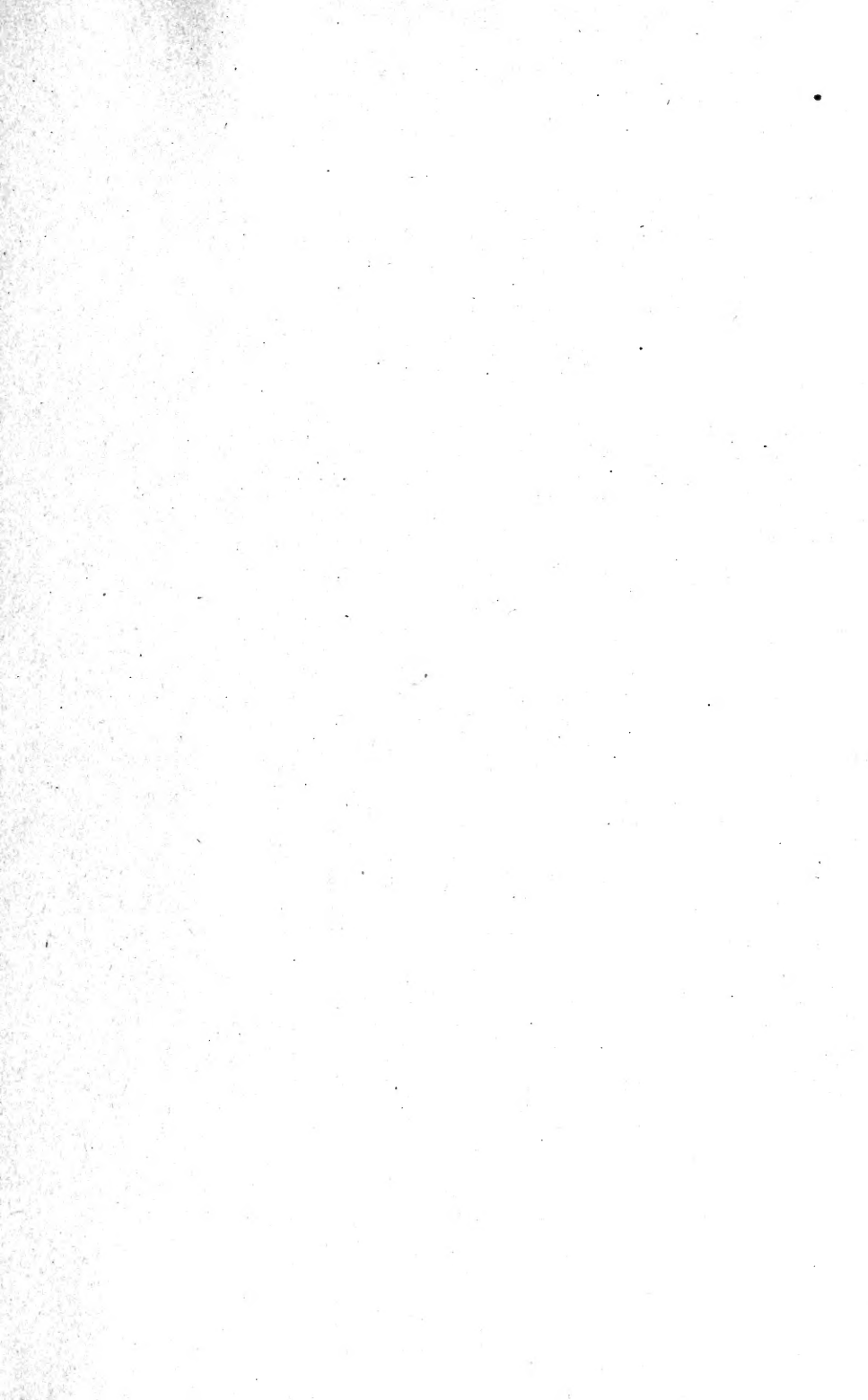
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